

ลักษณะเฉพาะของเสียดโลมาอิรวดี *Orcaella brevirostris* ในบ่อเลี้ยง



นายเทวฤทธิ์ สวารชร

จุฬาลงกรณ์มหาวิทยาลัย

CHULALONGKORN UNIVERSITY

บทคัดย่อและแฟ้มข้อมูลฉบับเต็มของวิทยานิพนธ์ตั้งแต่ปีการศึกษา 2554 ที่ให้บริการในคลังปัญญาจุฬาฯ (CUIR)

เป็นแฟ้มข้อมูลของนิสิตเจ้าของวิทยานิพนธ์ ที่ส่งผ่านทางบัณฑิตวิทยาลัย

The abstract and full text of theses from the academic year 2011 in Chulalongkorn University Intellectual Repository (CUIR)

are the thesis authors' files submitted through the University Graduate School.

วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรมหาบัณฑิต

สาขาวิชาวิทยาศาสตร์ทางทะเล ภาควิชาวิทยาศาสตร์ทางทะเล

คณะวิทยาศาสตร์ จุฬาลงกรณ์มหาวิทยาลัย

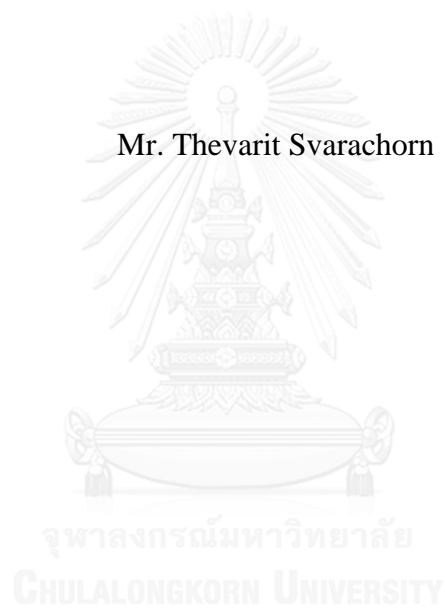
ปีการศึกษา 2558

ลิขสิทธิ์ของจุฬาลงกรณ์มหาวิทยาลัย

SOUND CHARACTERISTICS OF CAPTIVE IRRAWADDY DOLPHIN

Orcaella brevirostris

Mr. Thevarit Svarachorn



A Thesis Submitted in Partial Fulfillment of the Requirements
for the Degree of Master of Science Program in Marine Science

Department of Marine Science

Faculty of Science

Chulalongkorn University

Academic Year 2015

Copyright of Chulalongkorn University

Thesis Title	SOUND CHARACTERISTICS OF CAPTIVE IRRAWADDY DOLPHIN <i>Orcaella brevirostris</i>
By	Mr. Thevarit Svarachorn
Field of Study	Marine Science
Thesis Advisor	Jes Kettratad, Ph.D.
Thesis Co-Advisor	Associate Professor Doctor Nantarika Chansue

Accepted by the Faculty of Science, Chulalongkorn University in Partial
Fulfillment of the Requirements for the Master's Degree

..... Dean of the Faculty of Science
(Associate Professor Doctor Polkit Sangvanich)

THESIS COMMITTEE

..... Chairman
(Associate Professor Doctor Voranop Viyakarn)

..... Thesis Advisor
(Jes Kettratad, Ph.D.)

..... Thesis Co-Advisor
(Associate Professor Doctor Nantarika Chansue)

..... Examiner
(Assistant Professor Doctor Nuttakorn Thubthong)

..... External Examiner
(Kongkiat Kittiwattanawong, Ph.D.)

เทวฤทธิ์ สวารชร์ : ลักษณะเฉพาะของเสียงโลมาอิรวดี *Orcaella brevirostris* ในบ่อเลี้ยง (SOUND CHARACTERISTICS OF CAPTIVE IRRAWADDY DOLPHIN *Orcaella brevirostris*) อ.ที่ปริกษาวิทยานิพนธ์หลัก: อ. ดร. เจษฎ์ เกษตระทัต, อ.ที่ปริกษาวิทยานิพนธ์ร่วม: รศ. สพญ. ดร. นันทริกา ชันชื้อ, 79 หน้า.

การศึกษาเสียงร้องในโลมาอิรวดี (*Orcaella brevirostris*) มีมานานกว่าสามทศวรรษ แต่ทว่ายังมีข้อมูลที่สำคัญบางอย่างขาดหายไป โดยเฉพาะเสียงร้องของโลมาที่อยู่ในบ่อเลี้ยง ซึ่งสภาพแวดล้อมในที่ดังกล่าวสามารถสร้างผลกระทบต่อพฤติกรรมของโลมาได้เช่นกัน จากการสำรวจกว่า 40 ชั่วโมงในเดือนมีนาคมและพฤศจิกายน 2014 พบพฤติกรรมการส่งเสียงร้องเกือบ 7,000 ตัวอย่าง พบว่าเสียงร้องอันหลากหลายของโลมาอิรวดีในบ่อเลี้ยงนั้น สามารถจำแนกเป็นกลุ่มต่างๆได้แก่ “Clicks” 2 ชนิด (3,898 ตัวอย่าง), “Pulsed Sounds” 5 ชนิด (2,807 ตัวอย่าง) และ “Whistles” 9 ชนิด (44 ตัวอย่าง) ซึ่งเสียง Clicks จะใช้ในการนำทางที่พบเป็นปกติขณะโลมา กินอาหารและว่ายน้ำ ส่วนเสียง Pulsed Sounds สอดคล้องกับพฤติกรรมที่หลากหลายทั้งการสื่อสาร การเข้าสังคมและการมีปฏิสัมพันธ์ระหว่างโลมาด้วยกันเองหรือกับนักท่องเที่ยว รวมถึงการแสดงอารมณ์ต่างๆเช่น โกรธ ตื่นเต้น หรือแม้แต่เมื่อถูกกระตุ้นอารมณ์ทางเพศ ส่วน Whistles นั้นพบเป็นจำนวนน้อยมากเมื่อเทียบกับ Clicks และ Pulsed Sounds นอกจากนี้เสียง Whistles ในการศึกษาครั้งนี้มีความแตกต่างจาก Whistles ที่พบในโลมาในธรรมชาติเนื่องจากการปรับตัวในบ่อเลี้ยง พฤติกรรมการส่งเสียงร้องโดยรวมแล้วจะพบมากอย่างมีนัยสำคัญ ($p = 0.000009$) ในขณะที่โลมามีกิจกรรมว่ายน้ำและปฏิสัมพันธ์ร่วมกับนักท่องเที่ยว อย่างไรก็ตามงานวิจัยฉบับนี้คือการศึกษที่สามารถบันทึกเสียงร้องของโลมาอิรวดีได้ครบทั้งหมด 3 กลุ่มเป็นครั้งแรก และเป็นจุดเริ่มต้นการศึกษาเสียงร้องที่สอดคล้องกับพฤติกรรมของโลมาสายพันธุ์นี้ในบ่อเลี้ยงอีกด้วย

ภาควิชา วิทยาศาสตร์ทางทะเล

สาขาวิชา วิทยาศาสตร์ทางทะเล

ปีการศึกษา 2558

ลายมือชื่อนิติต

ลายมือชื่อ อ.ที่ปริกษาหลัก

ลายมือชื่อ อ.ที่ปริกษาร่วม

5571985723 : MAJOR MARINE SCIENCE

KEYWORDS: IRRAWADDY DOLPHIN / ORCAELLA BREVIROSTRIS / CETACEAN / SOUND / ACOUSTIC / VOCALIZATION / BEHAVIOUR / CAPTIVITY / SWIM-WITH-DOLPHIN PROGRAM

THEVARIT SVARACHORN: SOUND CHARACTERISTICS OF CAPTIVE IRRAWADDY DOLPHIN *Orcaella brevirostris*. ADVISOR: JES KETTRATAD, Ph.D., CO-ADVISOR: ASSOC. PROF. DR. NANTARIKA CHANSUE, 79 pp.

Even though there have been several studies on vocal repertoires and behaviours of Irrawaddy dolphins (*Orcaella brevirostris*) in recent decades, important pieces of information are still missing, especially the sounds produced in captivity where environmental differences can affect their physical and acoustic behaviours. Over 40 hours of observations in March and November 2014 with almost 7,000 vocalization samples, it was determined that the captive Irrawaddy dolphins produced various types of sound including two types of clicks ($n = 3,898$), five types of pulsed sounds ($n = 2,807$), and nine types of whistles ($n = 44$). This work also describes three newly discovered pulsed sounds and all nine whistles types in this species. Clicks were observed most frequently during feeding and swimming in navigational contexts. Pulsed sounds were mainly used in social or emotional contexts associated with various behaviours, even aggression, sexual arousal, and tourist-encounter. Whistles, on the other hand, were scarcely heard which might imply that the communication was not necessary. Whistling behaviour was contradictory to those reported for other wild delphinids which were potentially caused by habituation in captivity. Overall vocalizations, which were concurrent with activity levels, were recorded at a significantly higher rate ($p = 0.000009$) when tourists were present during “swim-with-dolphin” programs. This is the first study to correlate Irrawaddy dolphin’s sounds and behaviours in captivity and represents the first time that all three sound categories have been recorded for this species in captivity.

Department: Marine Science

Student's Signature

Field of Study: Marine Science

Advisor's Signature

Academic Year: 2015

Co-Advisor's Signature

ACKNOWLEDGEMENTS

Writing a thesis is just like making a motion picture, but more academic and less dramatic. It has been a long journey since I started this project in 2012, and the road to this thesis is by no means of any easiness, because I am the only one in Thailand who is interested in the research genre. Nevertheless, every epic motion picture needs a huge collaboration from diverse groups of people from various departments; same as this thesis, which could be accomplished by the supports from amazing people and organizations.

First of all, I would like to thank the Pattaya Dolphin World & Resort for allowing us to study their beloved dolphins. Thanks are also due to resort staff; especially, Dr. Nopphakarn Singkhum, the resort's authorized veterinarian, for their expediency and assistance during the research. This work was partially funded by the Development and Promotion of Science and Technology Talents Project (DPST | Royal Government of Thailand Scholarship) and The 90th Anniversary of Chulalongkorn University Fund (Ratchadaphiseksomphot Endowment Fund). Next, I would like to give my gratitude and my respects to Dr. Jes Kettratad for being an awesome advisor; to Assoc. Prof. Dr. Nantarika Chansue, Assist. Prof. Dr. Nuttakorn Thubthong, Dr. Kongkiat Kittiwattanawong, Mr. Wisit Leelasiriwong, and Assist. Prof. Dr. Tonphong Kaewkongkha, for every advice and technical supports.

In publication process, I would like to thank Dr. Kathleen M. Dudzinski and Dr. Elizabeth Henderson (editor and co-editor of Aquatic Mammals Journal), including all the reviewers and Prof. Francis G. Plumley, for their hardworking and for providing constructive comments and suggestions which greatly improved the manuscript. Also, I gratefully thank to many individuals who helped and supported this research along the whole process. Above all, I would like to personally thank all dearest friends from RorRae Group and family-like colleagues from Excellent Preparatory Academy (EPA) for the love and the support they gave.

CONTENTS

	Page
THAI ABSTRACT	iv
ENGLISH ABSTRACT.....	v
ACKNOWLEDGEMENTS	vi
CONTENTS.....	vii
FIGURE CONTENTS	1
TABLE CONTENTS.....	6
CHAPTER 1 INTRODUCTION	7
Objectives	9
Expected Outcomes	9
Literature Review	9
1. Irrawaddy Dolphin	9
2. Dolphin’s Sound Production Mechanism.....	11
3. Dolphin’s Sound Classification.....	13
3.1 Clicks.....	13
3.2 Pulsed Sounds.....	16
3.3 Whistles	20
4. Acoustic Research of Irrawaddy Dolphin	24
CHAPTER 2 METHODOLOGY	27
1. Study Site and Animals	27
2. Recording Equipment	27
3. Acoustic Data Collection.....	30
4. Behavioural Data Collection.....	30
5. Acoustic Data Analysis.....	39
6. Statistical Analysis.....	40
7. Behavioural Data Analysis	40
CHAPTER 3 RESULTS	41
1. Clicks	41
2. Pulsed Sounds.....	43

	Page
2.1 Crack	43
2.2 Creak	44
2.3 Raspberry.....	45
2.4 Scrabble	45
2.5 Squeak	46
3. Whistles	52
4. Vocalization Rate.....	53
CHAPTER 4 DISCUSSION.....	61
1. Clicks	61
2. Pulsed Sounds	62
2.1 Pulsed Sounds & Aggression	62
2.2 Pulsed Sounds & Sexual Arousal.....	63
2.4 Pulsed Sounds & Resting Behaviours	65
3. Whistles	66
CHAPTER 5 CONCLUSIONS	70
REFERENCES	72
VITA.....	79

FIGURE CONTENTS

Figure 1 Captive adult male Irrawaddy dolphin (<i>Orcaella brevirostris</i>) at Pattaya Dolphin World & Resort, Chonburi, Thailand	10
Figure 2 Schematic of a dolphin's head (Au, 2009)	12
Figure 3 A diagram of the MLDB complex and sound production structures in the head of a dolphin (Frankel, 2009).....	12
Figure 4 Spectrogram of clicks produced by wild Irrawaddy dolphin (<i>Orcaella brevirostris</i>) at Mahakam River, Indonesia (Kreb & Borsani, 2004)	14
Figure 5 Spectrogram of pulsed sounds produced by two captive bottlenose dolphins (<i>Tursiops truncatus</i>) during aggressive interactions (Blomqvist & Amundin, 2004)	16
Figure 6 Spectrogram of whistles produced by wild Baird's beaked whale (<i>Berardius bairdii</i>) (Dawson et al., 1998)	21
Figure 7 Top view of the dolphin's pool at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014	28
Figure 8 Top view of the dolphin's pool at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014	28
Figure 9 The Cetacean Research™ CR3 Hydrophone: an acoustic tool which was used for receiving all underwater sounds (frequency range: 0.0001-240 kHz, sensitivity: -210 dB, re 1V/μPa).	29
Figure 10 PreSonus AudioBox™ USB: while connecting to the hydrophone and the laptop, this sound recorder was used for recording the underwater sounds (maximum sampling rate = 44.1 kHz).	29
Figure 11 Tourists were participating for swimming and interacting with the dolphins in swim-with-dolphin programs during tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014.....	32
Figure 12 The pool's physical conditions during the non-tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014: tourists were absent, and only observer, trainers, and authorized staff were present in the pool area — all dolphins freely swam through all areas of the pool.	32
Figure 13 In both tourist and non-tourist sessions, acoustic data was recorded using the hydrophone (Cetacean Research™ CR3 Hydrophone) connected to a recording system (PreSonus AudioBox™ USB) and a laptop (SONY VAIO T Series). Behavioural data was recorded by video recording which was simultaneously done	

with sound recording using a video camera. The observer stayed at designated viewing areas about 3 m from the edge of the pool.....33

Figure 14 Feeding behaviour: captive male Irrawaddy dolphin (*Orcaella brevirostris*) consumed food items given by the trainer during tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014.34

Figure 15 Interaction behaviour: captive male Irrawaddy dolphin (*Orcaella brevirostris*) was engaged in physical contacts with the tourists or trainers — tourists were allowed to touch all body parts except the genital area during tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014.....34

Figure 16 Jumping behaviour: captive male Irrawaddy dolphin (*Orcaella brevirostris*) aerially jumped with partial or whole body displayed during tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014.....35

Figure 17 Playing behaviour: captive male Irrawaddy dolphin (*Orcaella brevirostris*) interacted with artificial objects such as balls and flying disc during tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014.....35

Figure 18 Socializing behavior: two captive male Irrawaddy dolphins (*Orcaella brevirostris*) socialized with one another including swimming along each other and having physical contacts during non-tourist-session at Pattaya Dolphin World & Resort in, Chonburi, Thailand March 2014 — any signs of aggressive or sexual orientations were excluded.36

Figure 19 Swimming behaviour: captive male Irrawaddy dolphin (*Orcaella brevirostris*) individually swam during non-tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014.36

Figure 20 Tourist-Encounter: captive male Irrawaddy dolphins (*Orcaella brevirostris*) spontaneously swam toward the tourists while they were entering or leaving the pool area, as well as while they were exchanging/relocating the stations within the pool during swim-with-dolphin programs during tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014.37

Figure 21 Water spitting: captive male dolphins (*Orcaella brevirostris*) spit water during tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 — although this is natural behaviour, it was never displayed unless the animals were directed to do so by their trainers.37

Figure 22 Sexual arousal behaviour: captive male Irrawaddy dolphin (*Orcaella brevirostris*) was sexually aroused by the dolphinarium's veterinarian at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014 — this behaviour

was conducted in private session where only the veterinarian and the observer were allowed to be present within the pool.38

Figure 23 Sexual arousal: captive male Irrawaddy dolphin (*Orcaella brevirostris*) were made to ejaculate by the dolphinarium’s veterinarian at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014 — this husbandry behaviour was trained in order to collect the sperm, and it was conducted in private session where only the veterinarian and the observer were allowed to be present within the pool....38

Figure 24 Spectrogram of “clicks with constant ICI” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.)42

Figure 25 Spectrogram of “clicks with fluctuating ICI” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.)42

Figure 26 Number of two clicks types (clicks with constant ICI and clicks with fluctuating ICI) produced by three captive male Irrawaddy dolphins (*Orcaella brevirostris*) at Pattaya Dolphin World & Resort, Chonburi, Thailand in March and November 2014.....43

Figure 27 Spectrogram of pulsed sound “crack” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 18 kHz was an anomaly produced by the recording system.)48

Figure 28 Spectrogram of pulsed sound “creak” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 18 kHz was an anomaly produced by the recording system.)48

Figure 29 Spectrogram of pulsed sound “raspberry” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.)49

Figure 30 Spectrogram of pulsed sound “scrabble” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.)49

- Figure 31** Spectrogram of pulsed sound “squeak” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.).....50
- Figure 32** Number of five pulsed sounds types (crack, creak, raspberry, scrabble, and squeak) produced by three captive male Irrawaddy dolphins (*Orcaella brevirostris*) at Pattaya Dolphin World & Resort, Chonburi, Thailand in March and November 2014.....50
- Figure 33** Continuous shots (A-D) of aggression behaviours displayed by two captive male Irrawaddy dolphins (*Orcaella brevirostris*) — one dolphin swam quickly and charged another dolphin by leaping on it at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014.51
- Figure 34** Spectrogram of whistle “shriek” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 18 kHz was an anomaly produced by the recording system.).....55
- Figure 35** Spectrogram of whistle “fall” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 18 kHz was an anomaly produced by the recording system.).....55
- Figure 36** Spectrogram of whistle “flat” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014 (The intense narrowband frequency at 18 kHz was an anomaly produced by the recording system.).....56
- Figure 37** Spectrogram of whistle “multi-flat” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014 (The intense narrowband frequency at 18 kHz was an anomaly produced by the recording system.).....56
- Figure 38** Spectrogram of whistle “breaker” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.).....57
- Figure 39** Spectrogram of whistle “chirp” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.).....57

- Figure 40** Spectrogram of whistle “harmonic” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.).....58
- Figure 41** Spectrogram of whistle “multi-chirp” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.)58
- Figure 42** Spectrogram of whistle “multi-loop” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.)59
- Figure 43** Number of nine whistles types (breaker, chirp, fall, flat, harmonic, multi-chirp, multi-flat, multi-loop, and shriek) produced by three captive male Irrawaddy dolphins (*Orcaella brevirostris*) at Pattaya Dolphin World & Resort, Chonburi, Thailand in March and November 201459
- Figure 44** Number of vocalization (clicks, pulsed sounds, and whistles) produced by three captive male Irrawaddy dolphins (*Orcaella brevirostris*) during tourist and non-tourist sessions at Pattaya Dolphin World & Resort, Chonburi, Thailand in March and November 201460
- Figure 45** Pulsed sounds rate (pulse/min) produced by three captive male Irrawaddy dolphins (*Orcaella brevirostris*) during tourist and non-tourist sessions at Pattaya Dolphin World & Resort, Chonburi, Thailand in March and November 2014 (The lines on the top of the bar graph represent the standard error.)60
- Figure 46** Spectrogram of an intense period of “pulsed sounds” rapidly produced by captive male Irrawaddy dolphin (*Orcaella brevirostris*) during tourist-encounter at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014.....64
- Figure 47** Resting behaviour/sleeping: the captive male Irrawaddy dolphins (*Orcaella brevirostris*) stopped swimming and stayed still while only the upper proportion of the head was displayed above the water surface during non-tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014.67
- Figure 48** Resting behaviour/slow swimming: the captive male Irrawaddy dolphin (*Orcaella brevirostris*) was swimming very slowly (almost staying still) while the upper proportion of the head and the body were displayed above the water surface during non-tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014.....67

TABLE CONTENTS

Table 1 Descriptive statistics for acoustic parameters of pulsed sounds (n = 2,807) with range and mean \pm sd, including the associated behaviours, produced by three captive male Irrawaddy dolphins (<i>Orcaella brevirostris</i>) at Pattaya Dolphin World & Resort, Chonburi, Thailand in March and November 2014	47
Table 2 Descriptive statistics for acoustic parameters of whistles (n = 44) with value given as mean \pm sd, including the associated behaviours, produced by three captive male Irrawaddy dolphins (<i>Orcaella brevirostris</i>) at Pattaya Dolphin World & Resort, Chonburi, Thailand in March and November 2014.....	54



CHAPTER 1

INTRODUCTION

It has been debated whether dolphins have their own language since ancient times. To begin decoding the language, we must understand the basic characteristics of the “call” which is an important component. Delphinid sounds are generally divided into three main categories: clicks, pulsed sounds, and whistles (Frankel, 2009). Clicks are mainly used for navigation by echolocation (Au, 2009). Pulsed sounds play important roles in communication, social context, and emotional expression (Herman & Tavolga, 1980; Overstrom, 1983; Herzing, 1988; Dawson, 1991; Connor & Smolker, 1996; Herzing, 1996; Janik, 2000b; Van Parijs & Corkeron, 2001; Lammers et al., 2006; Rankin et al., 2007). Whistles primarily serve in communication, self-identification, group cohesion, and social context (Sayigh et al., 1990; Smolker et al., 1993; Janik & Slater, 1998; Janik, 2000a; Rasmussen & Miller, 2002; Acevedo-Gutiérrez & Stienessen, 2004; Watwood et al., 2004; Díaz López & Shirai, 2009). Even though delphinid acoustic behaviours have been well studied all around the world for many decades, most of the previous research concentrated on bottlenose dolphins (*Tursiops* spp.) (Herzing, 1996; Janik, 2000b; Watwood et al., 2005; Janik et al., 2006; King et al., 2014). Thus, I am interested in vocalizations of a delphinid species distributed in Thailand, the Irrawaddy dolphins (*Orcaella brevirostris*).

Some studies have been conducted on the acoustic behaviour of Irrawaddy dolphins in both the wild and in captivity. The very first study in captivity discovered

only basic vocalizations, captured in short pulses called “pulse trains” with the dominant frequency of about 60 kHz (Kamminga et al., 1983). It is believed that pulsed trains are used for echolocation. No audible whistles were detected. Later, studies on riverine populations in the Mahakam River and Mekong River (Borsani, 1999) and a coastal population in Balikpapan Bay in East Kalimantan, Indonesia (Kreb & Borsani, 2004) found various types of broadband single and multiple clicks, broadband and narrowband pulsed sounds, and narrowband frequency-modulated whistles. The most recent study by Jensen et al. (2013) reported that Irrawaddy dolphins living in coastal and riverine habitats produced echolocation clicks with a centroid frequency around 95 kHz, high repetition rate (mean of 45 ms for inter-click interval), and low peak-to-peak source level (about 195 dB re 1 μ Pa at 1 m) compared to other wild delphinids. These differences may reflect an adaptation to the shallow freshwater habitats that are acoustically complex in structure, resulting in high reverberation and acoustic clutter. Although Van Parijs et al. (2000) described all the sound types belonging to an Irrawaddy dolphin population inhabiting coastal waters of northern Australia, they were later classified as Australian snubfin dolphin (*Orcaella heinsohni*) based on concordant character differences in morphology, osteology, and genetics (Beasley et al., 2002; Beasley et al., 2005). Hence, the primary objectives in this study were to characterize all sound types within 22 kHz produced by captive Irrawaddy dolphins. This study also represents an initial effort to understand delphinid behaviours corresponding to their vocalizations in captivity. I suggest that with enhancements this research field could begin to lay the groundwork that would benefit animal welfare.

Objectives

This research aims to record, describe, and characterize all sound types, including clicks, pulsed sounds, and whistles, produced by captive Irrawaddy dolphins. This study also represents an initial effort to understand the behaviours corresponding to the vocalizations in captivity of Irrawaddy dolphins.

Expected Outcomes

This is the first study to relate Irrawaddy dolphin's sounds to the behaviours in captivity. This work also represents the first time that all three sound categories have been recorded for this species in captivity which may lead to the discovery of unique acoustic patterns. Moreover, this captive study may give significant information to better understand the relationship between vocalizations and behaviours in order to compare to further studies in the wild. I also suggest that with enhancements this research field could begin to lay the groundwork that would benefit animal welfare which can be applied to conservative issue as well. Ultimately, this work is a part of initiation in dolphin's language decoding.

Literature Review

1. Irrawaddy Dolphin

“Irrawaddy dolphin” (*Orcaella brevirostris*) (Figure 1) is a marine mammal belongs to order Cetacea and family Delphinidae, and listed as vulnerable species by IUCN Red List. Irrawaddy dolphin populations occur in freshwater, brackish water, and saltwater found in rivers, estuaries, and coastal area from the east coast of India to Southeast Asia. However, the populations that occur in coastal water of northern

Australia and southern Papua New Guinea was recently described as “Australian snubfin dolphin” (*Orcaella heinsohni*), based on concordant character differences in external features, osteology, and genetics (Beasley et al., 2002; Beasley et al., 2005).



Figure 1 Captive adult male Irrawaddy dolphin (*Orcaella brevirostris*) at Pattaya Dolphin World & Resort, Chonburi, Thailand

Irrawaddy dolphin has a rounded head and the rostrum is absent, which make this dolphin obviously differ from other species. The dorsal fin is short, blunt, and triangular. The flippers are long and broad. The whole body is coloured in grey, but slightly pale on the underside than the back. At full maturity, age of 7-9 years, the body length is about 2.5 m for male and 2 m for female, and the weight is about 120 kg. Gestation lasts about 14 months and weaning occurs at about 2 years. Lifespan is about 30 years. The diets include fish, fish eggs, cephalopods, and crustaceans (Smith, 2009).

Irrawaddy dolphins are quite less active species than the others. Leaps are infrequent but occasionally occur when they are socializing or swimming against a strong current. Spyhopping, body rubbing, and tail slapping are sometimes observed. The dolphins occasionally spit streams of water from the mouth to a distance of 1-2 m. This unique behaviour is believed to be associated with feeding behaviour expelling water ingested during fish capture or possibly used herding fish. It was also suggested that it can be used in the context of social interactions (Smith et al., 1997).

2. Dolphin's Sound Production Mechanism

In 1980s, Cranford (1988) used modern X-ray computer tomography (CT) and magnetic resonance imaging techniques to study the internal structure within a dolphin's head (Figure 2). These techniques revealed the relative position, shape, and density of various internal structures, and eventually allowed Cranford to discover a structure called "monkey lip/dorsal bursae" (MLDB) which was the location of the sound generator. A decade later, the using of high-speed video simultaneously with hydrophone observations of acoustic signals also led Cranford et al. (1997) to discover two sets of structure "phonic lips" (previously referred to "monkey lips") located within the nasal complex, which their movements were synchronous to the sound production.

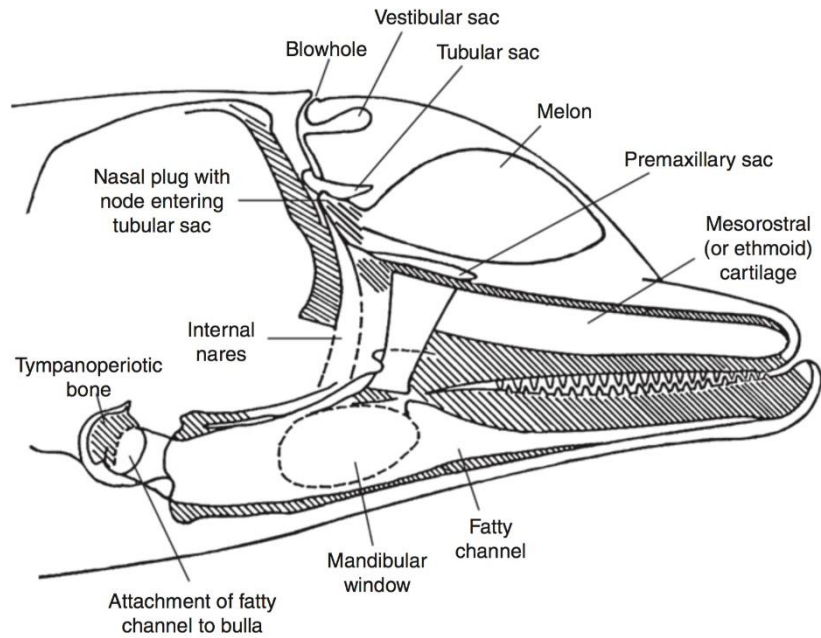


Figure 2 Schematic of a dolphin's head (Au, 2009)

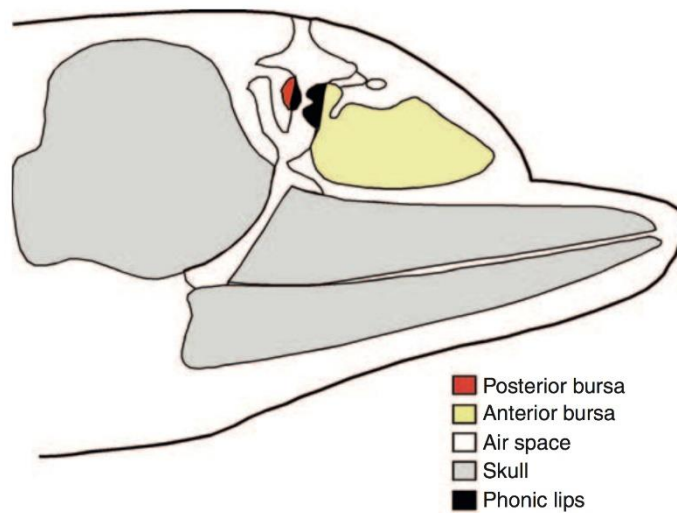


Figure 3 A diagram of the MLDB complex and sound production structures in the head of a dolphin (Frankel, 2009)

All delphinid species have two MLDB complexes located in the nasal complex below the blowhole at the upper portion of the head (Figure 3). Each MLDB complex is able to function independently, and simultaneously create different sounds from one another (Cranford, 2000). The MLDB complex consists of two lipid-filled sacs that connected to the phonic lips which protrude into the nasal passage. Delphinid sounds are created by the MLDB when the air is pushed from the air sacs and passes the phonic lips, which then open and slap shut, creating vibration. Then this vibration is transmitted through the “melon,” a lipid-rich tissue which acts like an acoustical lens that couples and focuses the sound into the water (Aroyan, 2001; Frankel, 2009).

3. Dolphin’s Sound Classification

Delphinids are well known to produce various kinds of sounds. Sounds produced by delphinids are categorized into three main types: clicks, pulsed sounds, and whistles (Frankel, 2009).

3.1 Clicks

Delphinids usually produced clicks (Figure 4) as a series, commonly referred to “click trains” (Popper, 1980). Clicks structures are varied among odontocetes which can be differentiated by frequency, duration, and waveform type (Tyack et al., 2006). Delphinid clicks are broadband and generally ranged from 60-120 kHz (Frankel, 2009). In Australian snubfin dolphin for instance, frequency range of click trains is above 22 kHz and the click rate is between 10-46 clicks/s. The duration varies from 0.5-11 s. Click trains were recorded most frequently during foraging and socializing (Van Parijs

et al., 2000). Irrawaddy dolphins, on the other hand, clicks frequency range around 80-100 kHz (Jensen et al., 2013) with the mean of 45 ms for inter-click interval.

Most of the delphinids are known to produce clicks. These clicks are used for echolocation, the process in which an animal obtains an assessment of its environment by emitting sounds and listening to echoes as the sound waves reflect off different objects in the environment (Au, 2009). Delphinids use echolocation for navigation and foraging, or even for avoiding predators (Au, 1993). With this unique ability, dolphins can determine size, shape, speed, distance, direction, and even some of the internal structure of objects in the water.

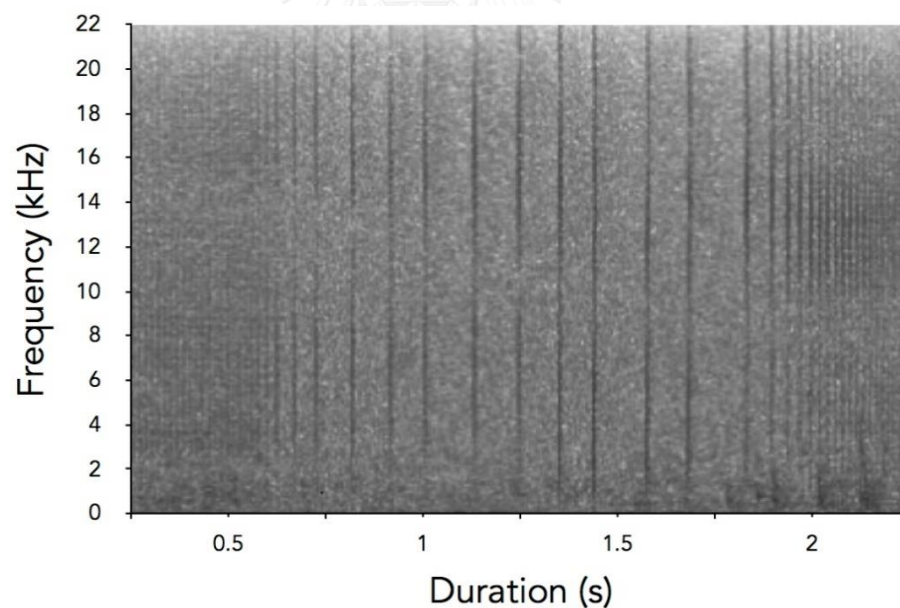


Figure 4 Spectrogram of clicks produced by wild Irrawaddy dolphin (*Orcaella brevirostris*) at Mahakam River, Indonesia (Kreb & Borsani, 2004)

The process of echolocation starts after clicks pass through the melon, which acts as an acoustical lens to focus these sound waves into a beam and projected forward

into water, these sound waves bounce off objects in the water and return to the dolphin in the form of an echo. The sounds are received and transmitted via fat-filled cavities of the lower jaw bones to the tympano-periotic bone, which contains the middle and inner ears. Then the sounds are transmitted in the form of nerve impulses via the auditory nerve to the brain, where the sounds information finally interpreted (Au, 2009).

Another different type of clicks called a “narrowband high frequency (NBHF) click” was found produced by porpoises, the genus *Cephalorhynchus*, part of the genus *Lagenorhynchus*, the pygmy sperm whale (*Kogia breviceps*) and Franciscana dolphin (*Pontoporia blainvillei*) (Morisaka & Connor, 2007). NBHF clicks have a narrow bandwidth, a high frequency around 130 kHz, but low power. The evolution of these NBHF clicks could be an anti-predation response to killer whales (*Orcinus orca*), who might not be able to hear them (Morisaka & Connor, 2007).

Delphinids are also capable to alter the spectral characteristics and source level of their clicks while echolocating (Frankel, 2009). At the beginning, delphinids usually emit louder clicks with higher repetition rate which generally possess more energy (Au & Würsig, 2004) to travel further through the media. Then the animals click softer in source level with lower repetition rate while approaching the targets (Au & Benoit-Bird, 2003) when they are located, since these clicks are simultaneously adjusted by emitting at the rate which allows the echo signals to return to the animals before the next click is emitted. In the end, the repetition rate is increasing again as the animals are getting closer to the targets (Au, 2009).

Nevertheless, clicks are various in characteristics among delphinids even within species due to environment. Therefore, I hypothesize that clicks produced by captive Irrawaddy dolphins may differ from previous studies, but NBHF will definitely not be recorded. Also the dolphins may not emit clicks often because they all have been habituated for four years in the captivity in which provide a clear visibility.

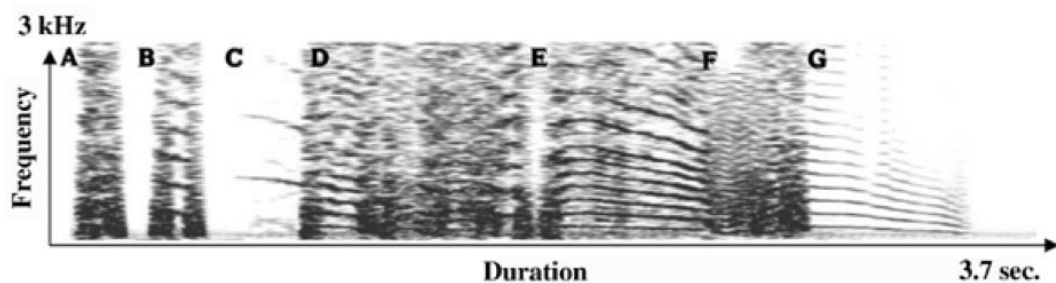


Figure 5 Spectrogram of pulsed sounds produced by two captive bottlenose dolphins (*Tursiops truncatus*) during aggressive interactions (Blomqvist & Amundin, 2004)

3.2 Pulsed Sounds

Pulsed sounds (Figure 5) are a series of broadband and narrowband pulses with short intervals (Frankel, 2009). Pulsed sounds can swiftly occur after one another that they might be perceived as continuous sound or even as clicks. The difference between them is that pulsed sounds are rapidly emitted as a series of high intensity clicks with extremely short inter-click interval which is regularly less than 10 ms (Lammers et al., 2006). As a result, they have been sometimes referring to as “high repetition-rate clicks” or “burst-pulse clicks” (Evans & Awbrey, 1984; Dawson, 1991; Rasmussen & Miller, 2002; Weir et al., 2007).

Most dephinids are capable of producing pulsed sounds, and one species can possess more than one pulse sound pattern. These unique sounds have been debated for their actual functionality, but most of the publications suggested that pulsed sounds play important roles in communication, social context, and emotional expression rather than echolocation (Herman & Tavolga, 1980; Popper, 1980; Overstrom, 1983; Herzing, 1988; Amundin, 1991; Dawson, 1991; Richardson et al., 1995; Connor & Smolker, 1996; Herzing, 1996; Murray et al., 1998; Janik, 2000b; Van Parijs & Corkeron, 2001; Lammers et al., 2006; Rankin et al., 2007).

Pulsed sounds are associated with various behaviours. Overstrom (1983) reported that pulsed sounds were related with aggressive behaviours in the bottlenose dolphins (*Tursiops truncatus*). This species also has been once reported using pulsed sounds “pop” during courtship and/or dominant behaviours (Connor & Smolker, 1996), and using “squawk” during sexual play (Herzing, 1996). As well as Atlantic spotted dolphins (*Stenalla frontalis*) which used high repetition-rate clicks labeled “buzz” and “squawk” during courtship and sexual play in respectively (Herzing, 1996). Furthermore, excessive noises were also recorded in spinner dolphins (*Stenella longirostris*) during copulation (Silva Jr et al., 2005). Thus, it is very interesting that if we understand how these pulsed sounds work, we might be able to develop acoustic devices to attract wild Irrawaddy dolphins to increase mating success, or population assessment all concerned in conservative issue.

Pulsed sounds can also occur in discrete pulses with very short duration which are referred to as “burst-pulsed sounds” (Frankel, 2009). Burst-pulsed sounds are produced by many odontocetes (tooth-whale) such as Hector’s dolphin

(*Cephalorhynchus hectori*) (Dawson, 1991), false killer whale (*Pseudorca crassidens*) (Murray et al., 1998), Australian snubfin dolphin (Van Parijs et al., 2000), Pacific humpback dolphin (*Sousa chinensis*) (Van Parijs & Corkeron, 2001), bottlenose dolphin (*Tursiops* spp.) (Blomqvist & Amundin, 2004), spinner dolphin (*Stenella longirostris*) (Lammers et al., 2006; Rossi-Santos et al., 2008), right whale dolphin (*Lissodelphis borealis*) (Rankin et al., 2007), sperm whale (*Physeter macrocephalus*) (Weir et al., 2007), killer whales (*Ornicus orca*) (Simon et al., 2007), dusky dolphin (*Lagenorhynchus obscurus*) (Au et al., 2010), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) (Henderson et al., 2011), and even non-whistling harbor porpoise (*Phocoena phocoena*) (Amundin, 1991).

Burst-pulsed sounds were exclusively observed during socializing and aggressive behaviours besides foraging according to numerous observations (Overstrom, 1983; Amundin, 1991; Dawson, 1991; Blomqvist & Amundin, 2004; Lammers et al., 2006). In Hector's dolphin (*Cephalorhynchus hectori*), high-repetition-rate burst-pulsed sounds, labeled "cries," were found abundantly produced during aerial and aggressive behaviour, suggesting that these cries were used in social contexts (Dawson, 1991). Amundin (1991) also reported that burst-pulsed sounds were associated in agonistic and distress situations in the harbor porpoise (*Phocoena phocoena*). Moreover, Hawaiian spinner dolphins (*Stenella longirostris*) were physically closer together when they produced burst-pulsed sounds than when they used whistles, suggesting a differential function between these two signals (Lammers et al., 2006). Nevertheless, Rankin et al. (2007) suggested that the stereotyped patterns of

burst-pulsed sounds described in right whale dolphins (*Lissodelphis borealis*) may have a communicative function similar to stereotyped whistles in other dolphins.

Interestingly, burst-pulsed sounds were suggested to be used as a sonic weapon (Norris & Mohl, 1983; Marten et al., 1988). With very high source level, pressure, and energy within the pulses, odontocetes may be capable of using these sounds to stun or temporarily immobilize their prey. Furthermore, in consideration of highly sensitive auditory system in Odontocetes (Au, 2009) combining with the fact that these burst-pulsed sounds are exclusively produced during aggression, it is possible that they are intentionally used to cause auditory distress in the antagonists. Those burst-pulsed sounds might be potentially used as acoustic weapon beside only used for expressing their animal's emotional states. This idea also conforms to what was proposed by (Blomqvist & Amundin, 2004) in captive bottlenose dolphins. Although, there still has no absolute evidence to confirm this idea, it surely is an interesting perspective. Hence, observations in natural habitats are preferred since no living preys are normally deployed in captivity, unless the further experiments are attempted in aquariums or dolphinariums.

Pulsed sounds produced by Irrawaddy dolphins are rarely studied in both physiology and actual functionality. Yet, there are few studies than mentioned about those produced by Irrawaddy dolphins and their relatives. Van Parijs et al. (2000) were able to record three different types of pulsed sounds produced by Australian snubfin dolphins: "creak," "buzz," and "squeak." They were all short in duration (0.1-4 s) and moderately high in repetition rate (44-116 pulses/s) with a frequency range above 22

kHz. Creaks and buzz were recorded during both foraging and socializing, whereas squeak was only heard when the dolphins were engaged in social behaviour. Later, Kreb & Borsani (2004) revealed various types of broadband “squeak” and “creak” and narrowband “grunt,” “moan,” and “quack” pulsed sounds. All of them were produced in extremely short duration (0.05-0.3 s) with incredibly high repetition rate (249-2019 pulses/s) and a frequency range above 22 kHz.

According to this, I initially hypothesize that pulsed sounds produced by captive Irrawaddy dolphins have high possibility to be found in various types related to diverse behaviours with frequency range above 22 kHz, and will be different in both repetition rate and duration from Australian snubfin dolphins and other wild populations. However, I predict that pulsed sounds recorded during the swim-with-dolphin programs will be recorded more frequently because exciting behaviours, socializing, communication, and emotional expression are likely to present more than resting and typical swimming periods. Also it is possible to discover a number of unique pulsed sounds patterns which can be newly described and named.

3.3 Whistles

Whistles (Figure 6) are narrowband frequency modulated sounds (Popper, 1980) with various contour patterns from short and simple chirps to long complex signals. Most delphinid species are able to produce whistles except those in the genus *Cephalorhynchus* (Morisaka & Connor, 2007). Delphinid whistles share many characteristics and it can be difficult to discriminate among them (Oswald et al., 2007). Until now, although the beginning-ending-minimum-maximum frequency and patterns

of frequency modulation are usually used as criteria, there are no universally accepted classifications for whistles (Frankel, 2009). In fact, all whistles among delphinids commonly share numerous characteristics including the fundamental frequency which is typically ranging between 1-30 kHz. Durations are most often between 0.5-1 s and can be as short as tens of millisecond, or as long as 3 s or more (Frankel, 2009).

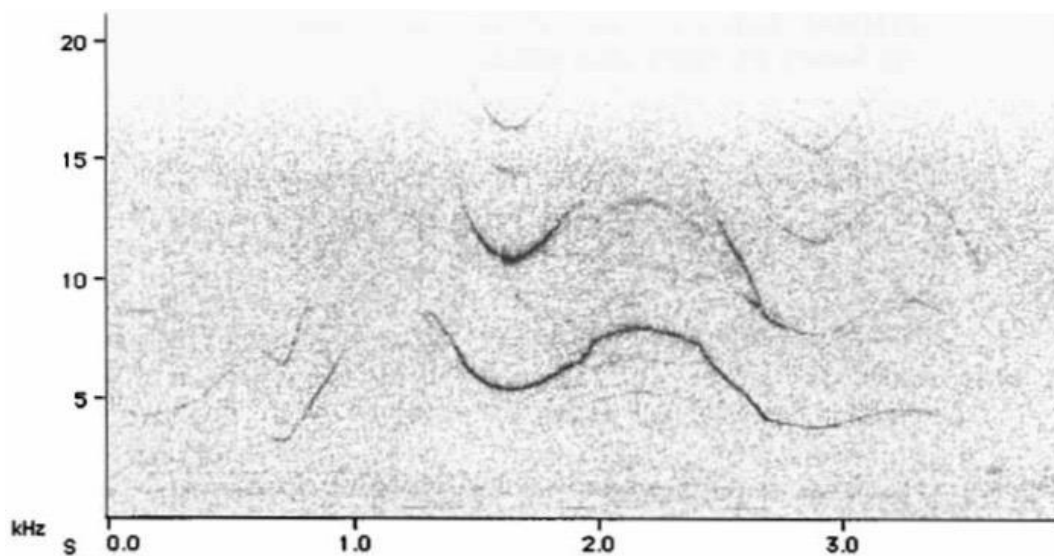


Figure 6 Spectrogram of whistles produced by wild Baird's beaked whale (*Berardius bairdii*) (Dawson et al., 1998)

In bottlenose dolphins (*Tursiops* spp.), researchers have found tens of distinct whistles (Deecke & Janik, 2006). In Australian snubfin dolphins, at least two whistle types were known to be produced. All are short in duration, low in frequency of 1-8 kHz, and simple in form compared with other delphinid species (Van Parijs et al., 2000). Recently, whistles produced by Irrawaddy dolphins have been revealed in various types of spectral contours, from simple to complex “harmonic” and “multi-

loop,” with the frequency ranging from 0.8-18.4 kHz and 0.05-0.3 s of duration (Kreb & Borsani, 2004).

Notwithstanding, Irrawaddy dolphin’s whistles seemed not to resemble to freshwater and marine tucuxis (Da Silva & Best, 1994; Azevedo & Simão, 2002; May-Collado & Wartzok, 2010) and Amazon River dolphin (*Inia geoffrensis*) (Wang et al., 1995) despite they all inhabit in similar environments. Nonetheless, the whistles were once discussed by Kreb & Borsani (2004) to have several similarities compared to other riverine species: Indus dolphin (*Platanista g. gangetica*) (Andersen & Pilleri, 1970; Pilleri et al., 1971), and Yangtze dolphin (*Lipotes vexillifer*) (Jing et al., 1981; Xiao & Jing, 1989). Moreover, riverine delphinids normally use lower frequency whistles compared to marine species, suggested that the low frequency whistles have better refractive capabilities suitable for the living in high suspended material habitats (Evans et al., 1988). Yet, the freshwater Ecuadorian boto (*Inia geoffrensis geoffrensis*) were reported for producing high frequency whistles up to 48.10 kHz (May-Collado & Wartzok, 2007). As for whistles produced by captive Irrawaddy dolphins, they are still questionable.

Whistles primarily serve in communication, self-identification, group cohesion, and social context (Caldwell et al., 1972; Sayigh et al., 1990; Smolker et al., 1993; Janik & Slater, 1998; Janik, 2000a; Rasmussen & Miller, 2002; Acevedo-Gutiérrez & Stienessen, 2004; Watwood et al., 2004; Díaz López & Shirai, 2009; Esch et al., 2009). Whistles usually present together with socializing and foraging (Van Parijs et al., 2000;

Podos et al., 2002; Krieb & Borsani, 2004; Au et al., 2010; May-Collado & Wartzok, 2010; Henderson et al., 2012; Andrade et al., 2015).

Numerous studies have shown that the whistling rate and complexity of the whistles are related to the behavioural context and excitement level (Norris et al., 1994; Herzing, 1996; Frankel, 2009). Delphinids tend to produce less frequent whistles and/or use the simple forms during low activity period when slow swimming, travelling, and resting (Weilgart & Whitehead, 1990; Sekiguchi & Kohshima, 2003). In contrary, frequent whistling and/or using whistles with complex forms were regularly recorded during high activity period: foraging, socializing, fast movement, and aerial behaviours (Herzing, 1996; Azevedo et al., 2010; Díaz López, 2011). In addition, the presence of excitement triggers such as boats and other delphinid groups can increase the whistling rate as well (Weilgart & Whitehead, 1990; Van Parijs & Corkeron, 2001; Krieb & Borsani, 2004). Whistling rate and other vocalization behaviours may also likewise relate to differences in age, social status, alertness, and gender (Norris et al., 1994).

Few delphinid species, especially bottlenose dolphins, can produce individually specific whistles contours called “signature whistles” (Caldwell & Caldwell, 1967; Caldwell et al., 1990; Sayigh et al., 1990; Sayigh & Janik, 2009; Sayigh & Janik, 2010). Signature whistles play an important role in social interactions, and are used to convey individual identity information that may be analogous to a “name” (Janik & Slater, 1998; Janik et al., 2006). They also function in maintaining group cohesion (Janik & Slater, 1998). Signature whistles is a learned behaviour; dolphin calves learn them within their first few months (about 4-6 months) from their mothers and retain them

their entire lives. Moreover, dolphins are also able to mimic the signature whistles of other individuals in their group in order to maintain social bonds (Frankel, 2009). Besides bottlenose dolphins, it has been suggested that Atlantic spotted dolphins (*Stenella frontalis*) (Herzing, 1996) and Pacific humpback dolphins (*Sousa* spp.) (Van Parijs & Corkeron, 2001) can produce them, and it is likely that additional species possess them as well. As poorly known about Irrawaddy dolphin's sounds, I doubt in their capability to produce signature whistles.

Ultimately, whistles produced by Irrawaddy dolphins are scarcely studied. So I preliminarily hypothesize that both whistles and signature whistles produced by captive Irrawaddy dolphins may dominant in low frequency below 30 kHz according to those recorded from Australian snubfin dolphins and those from Amazon River dolphins. However, I am unsure how many types of whistles I will able to record including the obscure signature whistles, but I expect that the dolphins will emit whistles more frequently and more complex forms during the swim-with-dolphin programs or high-activity periods, and when they are socializing.

4. Acoustic Research of Irrawaddy Dolphin

Over the last 60 years, acoustic behaviours of dolphins have been well studied in both captivity and the wild, and also continuously increasing in publication (McBride & Hebb, 1948; Caldwell & Caldwell, 1965; Herman & Tavolga, 1980; Sayigh et al., 1990; Janik, 2000a; Au et al., 2010; Andrade et al., 2015). Yet, most previous studies of delphinid sounds focused on bottlenose dolphins. Although little is known about acoustic behaviours of Irrawaddy dolphins in the wild and also in the captivity, there

have been a few studies. The very first study in captivity discovered only basic vocalizations, captured in short pulses of 25-30 μ sec called “pulse trains” with the dominant frequency of about 60 kHz (Kamminga et al., 1983) which was believed to be used for echolocation; however, no audible whistles were recorded. Later, studies on riverine populations in the Mahakam River and Mekong River (Borsani, 1999) and a coastal population in Balikpapan Bay in East Kalimantan, Indonesia (Kreb & Borsani, 2004) found various types of clicks, pulsed sounds, and whistles. The most recent study by Jensen et al. (2013) reported that Irrawaddy dolphins living in coastal and riverine habitats produced echolocation clicks with a centroid frequency around 95 kHz, high repetition rate (mean of 45 ms for inter-click interval), and low peak-to-peak source level (about 195 dB re 1 μ Pa at 1 m) compared to other wild delphinids. These differences may reflect to an adaptation to the shallow freshwater habitats that are acoustically complex in structure, resulting in high reverberation and acoustic clutter. Even though Van Parijs et al. (2000) described all the sound types belonging to an Irrawaddy dolphin population inhabiting coastal waters of northern Australia, they were later classified as Australian snubfin dolphin (Beasley et al., 2002; Beasley et al., 2005). Consequently, this study is the first to record all three sound categories. This represents the first time that all three sound categories for this species in captivity.

Studies of captive delphinids have contributed greatly towards our understanding of the acoustic behaviour, although studies of wild delphinids in their natural environment complement captivity studies by revealing how they use sounds in the wild where natural habitats have so much different characteristics from captive settings. Captive studies, on the other hand, also provide the fundamental knowledge

and theories for further applications, and even exhibit the effects of captivity that bring about changes in animals' physical and acoustic behaviours through time, which can be considered as a conservative issue. Here, this research describes the acoustic repertoire and vocalizations associated with behaviours recorded from a captivity population of Irrawaddy dolphins in Thailand.



CHAPTER 2

METHODOLOGY

1. Study Site and Animals

Three male Irrawaddy dolphins were studied in captivity at Pattaya Dolphin World & Resort, Chonburi Province, Thailand (Figure 7-8). All were adults with an average age of 30 years, all were in good health, and each had been habituated to the pool for four years. Each dolphin was identified by the shape of its dorsal fin, scars and natural marks on the dorsal fin and surrounding area. The resort pool was made of concrete, and was irregular in shape (pear-like). It was about 25 m in width and 50 m in length. The pool's depth varied from 5-6 m. The 6,000 m³ of re-circulated seawater had poor visibility out to about 2 m. The pool was divided into three stations, each with a swim platform for tourists to sit during "swim-with-dolphin" programs (SWD).

2. Recording Equipment

Acoustic recordings of underwater sounds were made using The Cetacean ResearchTM CR3 hydrophone (frequency range: 0.0001-240 kHz, sensitivity: -210 dB, re 1V/ μ Pa) (Figure 9) connected to a PreSonus AudioBoxTM USB recording system (frequency response: 14 Hz to 70 kHz \pm 3.0 dB) (Figure 10) at the sample rate of 44.1 kHz, and recorded in wav file on a SONY VAIO T Series laptop on Microsoft Windows[®] 8.1 operating system. Video recording was done using SONY Cyber-shot DSC-WX1 and iPad Air



Figure 7 Top view of the dolphin's pool at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014



Figure 8 Top view of the dolphin's pool at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014



Figure 9 The Cetacean Research™ CR3 Hydrophone: an acoustic tool which was used for receiving all underwater sounds (frequency range: 0.0001-240 kHz, sensitivity: -210 dB, re 1V/ μ Pa).



Figure 10 PreSonus AudioBox™ USB: while connecting to the hydrophone and the laptop, this sound recorder was used for recording the underwater sounds (maximum sampling rate = 44.1 kHz).

3. Acoustic Data Collection

Observations were conducted for 5 days in March and 10 days in November 2014. The only observation time allowed to take place was from 0830 to 1730 h. Acoustic recordings were collected during two sessions: (1) tourist session when tourists were present in the pool area, and were participated in SWD — each dolphin stayed at one station, and its sounds were obtained individually (Figure 11); (2) non-tourist session when tourists were absent, and only observer, trainers, and authorized staff were present in the pool area — all dolphins freely swam through all areas of the pool (Figure 12). A typical day included five rounds each of tourist and non-tourist sessions, but varied depending on the number of tourists present. The total observation time was approximately 42 hours. In both tourist and non-tourist sessions, the sounds were recorded on the hydrophone at a depth of 2 m while the observers stayed at designated viewing areas about 3 m from the edge of the pool.

4. Behavioural Data Collection

Behavioural data was continuously recorded by video camera concurrently with the acoustic recordings (Figure 13). According to preliminary observations, various behaviours exhibited in both tourist and non-tourist sessions generally fell into nine categories including: (1) Feeding: dolphins consumed food items (Figure 14); (2) Interaction: dolphins were engaged in physical contacts with the tourists or trainers (Figure 15) — tourists were allowed to touch all body parts except the genital area; (3) Jumping: dolphins aerially jumped with partial or whole body displayed (Figure 16); (4) Playing: dolphins interacted with artificial objects: e.g. balls and flying disc (Figure 17); (5) Socializing: dolphins socialized with one another including swimming along

each other and having physical contacts (Figure 18) — any signs of aggressive or sexual orientations were excluded; (6) Swimming: dolphins individually swam (Figure 19); (7) Tourist-Encounter: the dolphins spontaneously swam toward the tourists while they were entering or leaving the pool area, as well as while they were exchanging/relocating the stations within the pool during SWD (Figure 20); (8) Water Spitting: dolphins spit water (Figure 21) — although this is natural behaviour, it was never displayed unless the animals were so ordered; and (9) Sexual Arousal: male dolphins were stimulated to ejaculate by the dolphinarium's veterinarian — this husbandry behaviour was trained in order to collect the sperm, and it was conducted in private session where only the veterinarian and the observer were allowed to be present within the pool (Figure 22-23).

From these behaviours, only feeding, jumping, and playing were trained behaviours; dolphins were ordered by hand signals from the trainers to perform each behaviour. Additional behaviours were observed beyond these, and will be described in the results.

All experiments and observations were granted permission by the dolphinarium, and were conducted under direct supervision of an authorized veterinarian. This research was approved by Chulalongkorn University Institutional Animal Care and Use Committees (IACUC) and received the protocol number 1423004.



Figure 11 Tourists were participating for swimming and interacting with the dolphins in swim-with-dolphin programs during tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014.



Figure 12 The pool's physical conditions during the non-tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014: tourists were absent, and only observer, trainers, and authorized staff were present in the pool area — all dolphins freely swam through all areas of the pool.



Figure 13 In both tourist and non-tourist sessions, acoustic data was recorded using the hydrophone (Cetacean Research™ CR3 Hydrophone) connected to a recording system (PreSonus AudioBox™ USB) and a laptop (SONY VAIO T Series). Behavioural data was recorded by video recording which was simultaneously done with sound recording using a video camera. The observer stayed at designated viewing areas about 3 m from the edge of the pool.



Figure 14 Feeding behaviour: captive male Irrawaddy dolphin (*Orcaella brevirostris*) consumed food items given by the trainer during tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014.

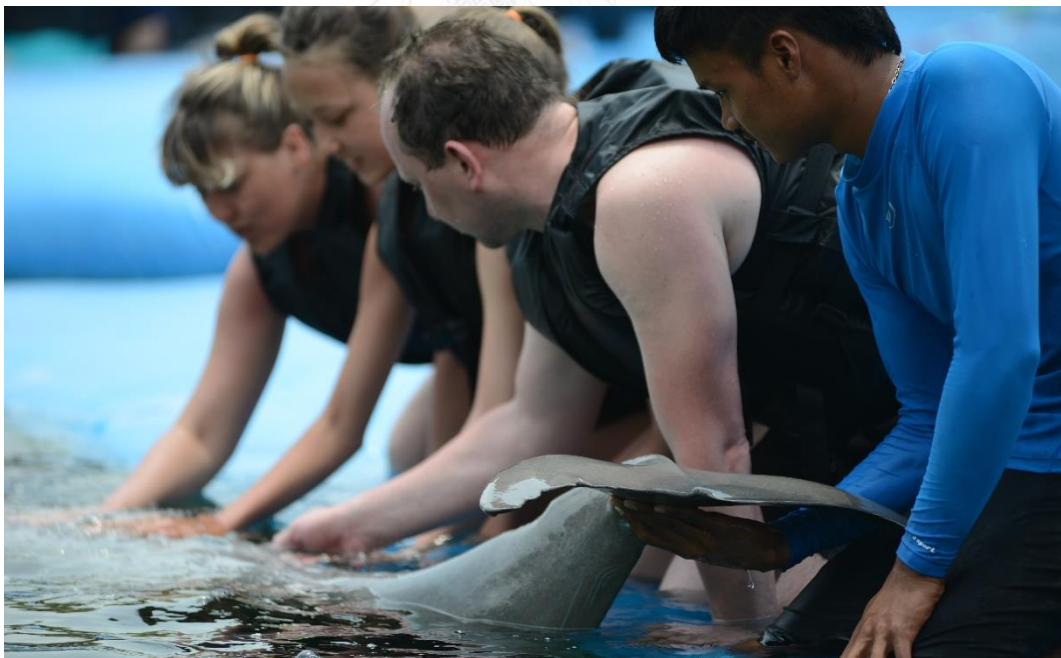


Figure 15 Interaction behaviour: captive male Irrawaddy dolphin (*Orcaella brevirostris*) was engaged in physical contacts with the tourists or trainers — tourists were allowed to touch all body parts except the genital area during tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014.



Figure 16 Jumping behaviour: captive male Irrawaddy dolphin (*Orcaella brevirostris*) aerially jumped with partial or whole body displayed during tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014.



Figure 17 Playing behaviour: captive male Irrawaddy dolphin (*Orcaella brevirostris*) interacted with artificial objects such as balls and flying disc during tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014.



Figure 18 Socializing behavior: two captive male Irrawaddy dolphins (*Orcaella brevirostris*) socialized with one another including swimming along each other and having physical contacts during non-tourist-session at Pattaya Dolphin World & Resort in, Chonburi, Thailand March 2014 — any signs of aggressive or sexual orientations were excluded.



Figure 19 Swimming behaviour: captive male Irrawaddy dolphin (*Orcaella brevirostris*) individually swam during non-tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014.



Figure 20 Tourist-Encounter: captive male Irrawaddy dolphins (*Orcaella brevirostris*) spontaneously swam toward the tourists while they were entering or leaving the pool area, as well as while they were exchanging/relocating the stations within the pool during swim-with-dolphin programs during tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014.



Figure 21 Water spitting: captive male dolphins (*Orcaella brevirostris*) spit water during tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 — although this is natural behaviour, it was never displayed unless the animals were directed to do so by their trainers.



Figure 22 Sexual arousal behaviour: captive male Irrawaddy dolphin (*Orcaella brevirostris*) was sexually aroused by the dolphinarium's veterinarian at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014 — this behaviour was conducted in private session where only the veterinarian and the observer were allowed to be present within the pool.



Figure 23 Sexual arousal: captive male Irrawaddy dolphin (*Orcaella brevirostris*) were made to ejaculate by the dolphinarium's veterinarian at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014 — this husbandry behaviour was trained in order to collect the sperm, and it was conducted in private session where only the veterinarian and the observer were allowed to be present within the pool.

5. Acoustic Data Analysis

The acoustic data was digitized as wideband spectrograms and waveforms using Adobe® Audition® CC (Version 6.0) and Praat (Version 5.3.66). In Adobe® Audition® CC (Version 6.0), the spectral displays of wideband spectrograms were analyzed based on following configurations: (1) windowing function = Blackman-Harris; (2) frequency display (spectral resolution = 512 | decibel range = 132 dB); and (3) pitch display (spectral resolution = 2,048 | decibel range = 75 dB).

Then sound data was divided into three main categories: clicks, pulsed sounds, and whistles. Only good signals, based on individual spectrogram's qualities where all parameters of the spectral contour (spectrogram shape) were distinctly measurable, were used for the further numerical analysis. After initial characterization, clicks and pulsed sounds were further analyzed statistically based on the following parameters: duration, click/pulse rate, repetition rate, frequency range, minimum frequency, maximum frequency, dominant frequency, inter-click interval (ICI), and number of harmonic structure within pulses. For whistles, the start frequency, end frequency, number of harmonics, and the modulation of frequency were also measured in addition to the other metrics described. However, each whistles type was classified based on the spectrogram shape only.

To analyze the vocalization rates, all sounds produced by captive Irrawaddy dolphins were divided into two groups based on the time periods they were made: (1) tourist session and (2) non-tourist session. The vocalization rate in each section from both tourist and non-tourist sessions was standardized into the unit of number of sound

produced per minute. Then the statistical analysis was made to determine the differences between vocalization rate between tourist and non-tourist session.

6. Statistical Analysis

All statistical analysis was performed in Statgraphics® (Centurion XV.II). The multiple comparison test (Dwass, 1960) or Kruskal-Wallis test (Kruskal & Wallis, 1952) were used to test whether there was a significant difference between the means of each parameter within each sound type during tourist and non-tourist sessions. The Two-Sample *t*-Test was used to determine if there were differences in means of vocalization rates (number of sounds produced per minute) in each sound type and overall sounds produced by captive Irrawaddy dolphins between tourist and non-tourist sessions

7. Behavioural Data Analysis

The video-recorded behavioural data was visually analyzed together with the acoustic data. Each behaviour associated with a vocalization was determined by time-lapsing the behaviours and the recorded vocalizations.

CHAPTER 3

RESULTS

From over 42 hours of acoustic recording, I obtained a total of 6,749 vocalization samples, which consisted of clicks (n = 3,898), pulsed sounds (n = 2,807), and whistles (n = 44). All of the values reported below are in the form of range (mean \pm standard deviation).

1. Clicks

Clicks were found in series of clicks commonly referred to as “click trains.” Clicks were broadband in frequency with a range from 0.3 kHz to above 22 kHz. The minimum frequency was 0.3-18.7 kHz (6.9 ± 2.3). Each click train consisted of 2-702 clicks (59.5 ± 75.9); the repetition rate was 1-882 clicks/s (37.4 ± 38.2). The duration was incredibly wide in range from 8 ms to 19 s (1.9 ± 2.3 s). Clicks were recorded mostly during feeding, followed by socializing and swimming. Clicks were produced significantly more ($p < 0.05$) during the tourist sessions.

Clicks were divided into two types (Figures 24-26) based on differences of the repetition rate or ICI patterns within the train: (1) clicks with constant ICI (n = 995) (Figure 24), and (2) clicks with fluctuating ICI (n = 2,903) (Figure 25). Co-analysis of video recording revealed that clicks with constant ICI were usually used for orientation and common navigation to locate unknown objects or the surrounding environment; clicks with fluctuating ICI were used while dolphins were approaching targets such as

fish thrown by the trainers during feeding, or artificial objects and tourists. Clicks with fluctuating ICI usually started with high repetition rate followed by low repetition rate and ended with high repetition rate (Figure 25).

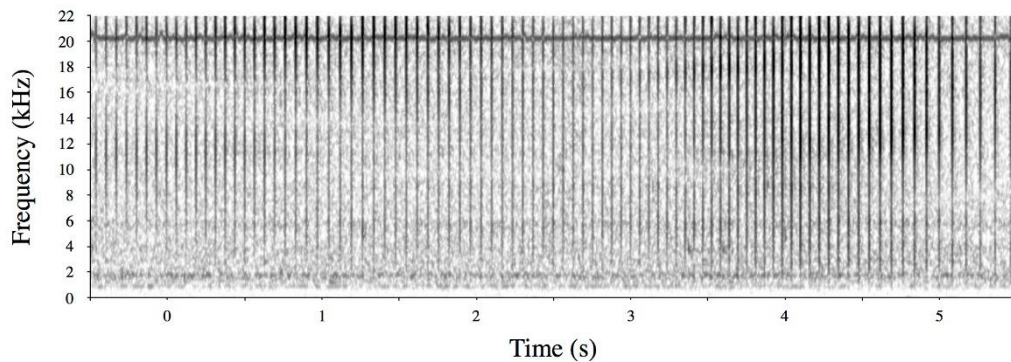


Figure 24 Spectrogram of “clicks with constant ICI” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.)

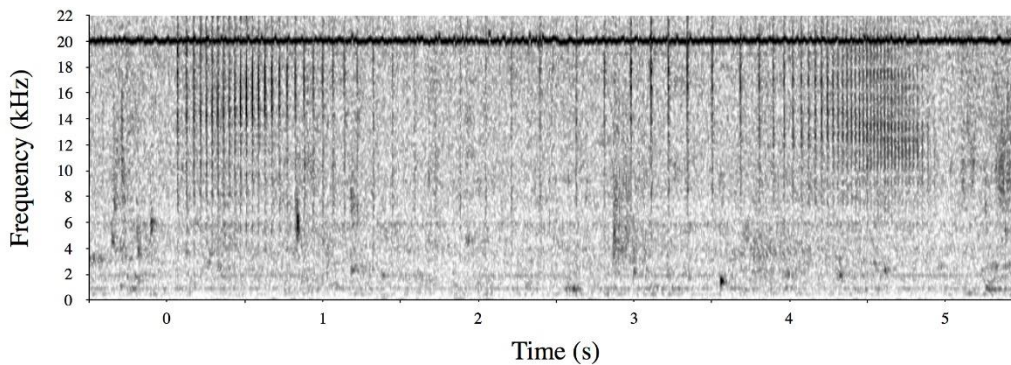


Figure 25 Spectrogram of “clicks with fluctuating ICI” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.)

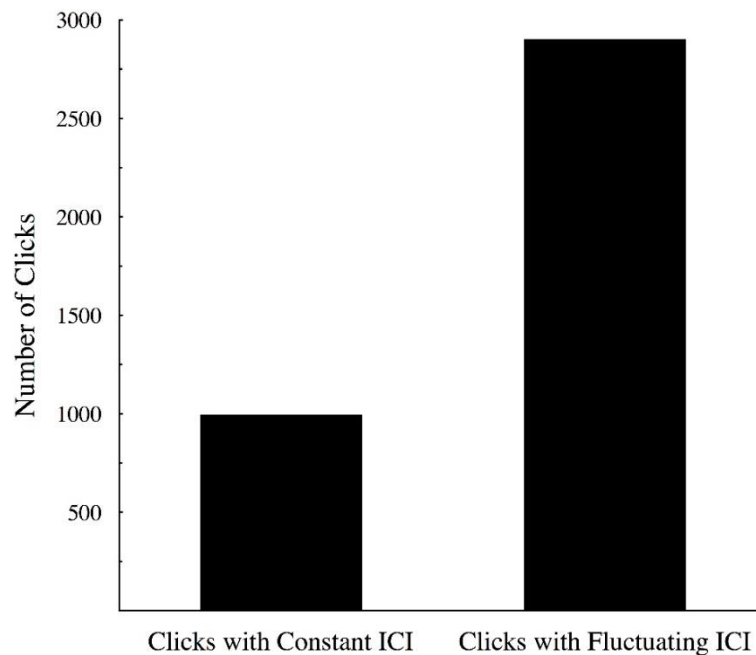


Figure 26 Number of two clicks types (clicks with constant ICI and clicks with fluctuating ICI) produced by three captive male Irrawaddy dolphins (*Orcaella brevirostris*) at Pattaya Dolphin World & Resort, Chonburi, Thailand in March and November 2014

2. Pulsed Sounds

Pulsed sounds consisted of both narrowband and broadband frequencies. There were five types of pulsed sounds (Figures 27-32 & Table 1). Pulsed sounds were different from each other primarily in pulse rate and repetition rate, followed by minimum frequency and ICI. Dolphins produced significantly more ($p < 0.05$) pulsed sounds during tourist session.

2.1 Crack

Cracks (Figure 27), the newly described pulsed sounds, had a unique sound like door creaking and were short broadband pulses with a frequency ranged from 0.1 kHz

to above 22 kHz. Cracks consisted of 1-192 pulses (17.9 ± 16) with a repetition rate of 1-477 pulses/s (69.9 ± 35.5). Cracks had low minimum frequency at 0.1-16 kHz (1.7 ± 1.1), and short duration lasted from 7 ms to 3.5 s (0.3 ± 0.3 s), and narrow ICIs with 1-395 ms (17.4 ± 31.7). Cracks also had a fluctuating ICI within a pulse, which is similar to clicks with fluctuating ICIs, but no distinct ICI patterns could be determined. Cracks ($n = 1,900$) were heard the most compared to other pulsed sounds, and were emitted significantly more often ($p < 0.05$) when tourists were present in the pool area, particularly when the dolphins were playing with balls and flying discs, and during tourist-encounter. Cracks were also produced simultaneously along with various behaviours: interactions with humans, feeding, jumping, swimming, and even when being ejaculated.

2.2 Creak

Creaks (Figure 28) were narrowband pulsed sounds with continuous wave-like structure and sound similar to buzzing sound. Creaks produced by captive Irrawaddy dolphins resembled those produced by wild Irrawaddy dolphins (Kreb & Borsani, 2004). Creaks were emitted in frequency ranged from 0.2 kHz to above 22 kHz. Creaks consisted of 2-73 pulses (26.5 ± 16.3) with a high repetition rate of 16-842 pulses/s (136.6 ± 117.4), and were 4 ms to 1.6 s in duration (0.2 ± 0.2 s). The minimum frequency was 0.2-7.7 kHz (1.7 ± 0.9). Creaks looked similar to cracks, but the duration, pulse rate, and repetition rate were significantly different ($p < 0.05$). Creaks ($n = 458$) were produced in association with several behaviours during tourist sessions: interaction, playing, feeding, water spitting, and jumping.

2.3 Raspberry

Raspberries (Figure 29) were broadband pulses with a frequency ranged from 0.1 kHz to above 22 kHz. Raspberries consisted of 2-57 pulses (15.9 ± 10.3) with a repetition rate of 15-347 pulses/s (64.3 ± 35.1). Raspberries had ICIs ranging from 1-210 ms (8.6 ± 16.1) with a minimum frequency at 0.1-8.7 kHz (1.5 ± 0.7) and a duration of 30 ms to 1.4 s (0.3 ± 0.2 s). The ICIs of raspberries differed from those in other pulsed sounds by two main characteristics: (1) they were broadband signals with constant ICIs (which varied among individuals) and (2) they were shorter than other pulsed sounds, with exception to “scrabble.” Raspberries also had significant differences ($p < 0.05$) from other pulsed sounds in two acoustic parameters: pulse rate and repetition rate. Raspberries ($n = 380$) were recorded mostly during tourist-encounter, and were also recorded along with following behaviours: interaction, jumping, playing, water spitting, and feeding. The name “raspberry” previously referred to a type of pulsed sounds produced by several delphinids (Herzing, 2000); however, there was no description of any acoustic parameter in the study, except the less than 1 s of the duration. Thus, I opted to use this name for the pulsed sound described above in order to describe its rasp-like-sound characteristic.

2.4 Scrabble

Scrabbles (Figure 30), another newly described pulsed sounds, were broadband pulses with a frequency ranged from 0.5 kHz to above 22 kHz with a minimum frequency at 0.5-3.5 kHz (1.6 ± 0.8). Scrabbles consisted of 4-200 pulses (31.1 ± 24.3) with a repetition rate of 29-181 pulses/s (91.4 ± 28.9) and a duration of 85 ms - 1.8 s (0.3 ± 0.2 s). Generally, scrabbles looked similar to cracks, however, scrabbles had

extremely narrow ICIs, 1-9 ms (1.9 ± 1.7). Moreover, among the broadband types, scrabbles had the shortest ICI and highest pulse rate. Thus, I used these parameters to exclude scrabbles from the other pulsed sounds. Scrabbles ($n = 66$) were produced most during playing, tourist-encounter, and interaction.

2.5 Squeak

Squeaks (Figure 31) were narrowband signals that were clearly distinct from the other pulsed sounds as distinguished by their loud-trumpet-like sounds and unique spectral contours displayed by a complicated stacking of harmonic structures. Since squeaks occurred in a single loud burst of sound which may be referred to as “burst-pulses” in many species (Herzing, 2000; Frankel, 2009), they were considered to be true burst-pulsed sounds for Irrawaddy dolphins. Squeaks were composed of multiple harmonics of narrowband frequency with very low minimum frequency of 0.1-0.2 kHz (0.1 ± 0.06), and bandwidth ranged from 0.1 kHz to above 22 kHz. Each squeak consisted of 52-62 pulses (56 ± 5.3) with very high repetition rate of 147-278 pulses/s (232.7 ± 74.0), and lasted between 0.1 and 0.5 s (0.3 ± 0.1) in duration. Squeaks had the highest mean repetition rate compared to all pulsed sounds, and the highest mean pulse rate among narrowband pulsed sounds. Only three squeaks were recorded; all were presented exclusively when aggressive behaviours were displayed; one dolphin swam quickly and charged another dolphin by leaping on it (Figure 33).

Table 1 Descriptive statistics for acoustic parameters of pulsed sounds (n = 2,807) with range and mean \pm sd, including the associated behaviours, produced by three captive male Irrawaddy dolphins (*Orcaella brevirostris*) at Pattaya Dolphin World & Resort, Chonburi, Thailand in March and November 2014

Category	Signal Type	Number (T NT)	Duration (s)	Pulse Rate (pulses)	Repetition Rate (pulses/s)	Inter-Click Interval (ms)	Frequency Range (kHz)	Minimum Frequency (kHz)	Maximum Frequency (kHz)	Behaviour
Crack	Broadband	1900 (1,780 120)	<0.1 - 3.5 (0.3 \pm 0.3)	1 - 192 (17.9 \pm 16)	1 - 477 (69.9 \pm 35.5)	1 - 395 (17.4 \pm 31.7)	0.1 - > 22	0.1 - 16 (1.7 \pm 1.1)	> 22	F, I, J, P, S, SA, So, TE, W
Creak	Narrowband	458 (451 7)	<0.1 - 1.6 (0.2 \pm 0.2)	2 - 73 (26.5 \pm 16.3)	16 - 842 (136.6 \pm 117.4)	-	0.2 - > 22	0.2 - 7.7 (1.7 \pm 0.9)	> 22	F, I, J, P, TE, W
Raspberry	Broadband	380 (376 4)	<0.1 - 1.4 (0.3 \pm 0.2)	2 - 57 (15.9 \pm 10.3)	15 - 347 (64.3 \pm 35.1)	1 - 210 (8.6 \pm 16.1)	0.1 - > 22	0.1 - 8.7 (1.5 \pm 0.7)	> 22	F, I, J, P, So, TE, W
Scrabble	Broadband	66 (58 8)	<0.1 - 1.8 (0.3 \pm 0.2)	4 - 200 (31.1 \pm 24.3)	29 - 181 (91.4 \pm 28.9)	1 - 9 (1.9 \pm 1.7)	0.5 - > 22	0.5 - 3.5 (1.6 \pm 0.8)	> 22	I, P, SA, TE
Squeak	Narrowband	3 (0 3)	0.1 - 0.5 (0.3 \pm 0.1)	52 - 62 (56 \pm 5.3)	147 - 278 (232.7 \pm 74.0)	-	0.1 - > 22	0.1 - 0.2 (0.1 \pm 0.06)	> 22	A

Number: T = tourist session and NT = non-tourist session; Behaviours: A = aggression; F = feeding; I = interaction/physical contact; J = jumping; P = playing; S = swimming; SA = sexual arousal; So = socializing; TE = tourist-encounter; W = water spitting

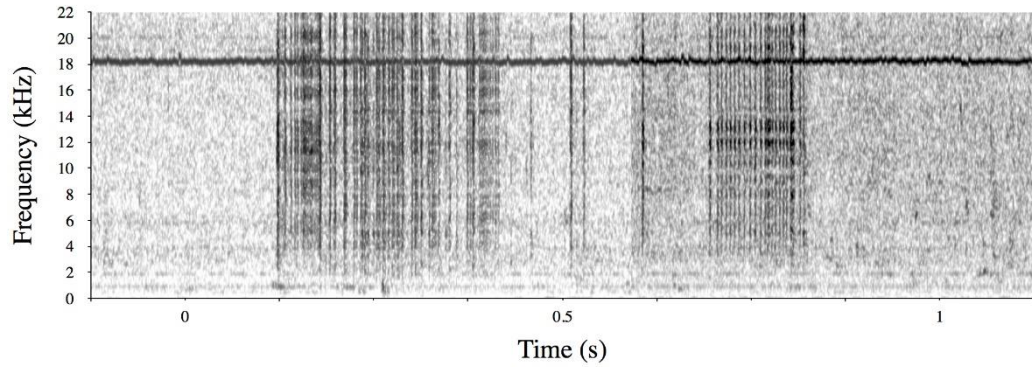


Figure 27 Spectrogram of pulsed sound “crack” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 18 kHz was an anomaly produced by the recording system.)

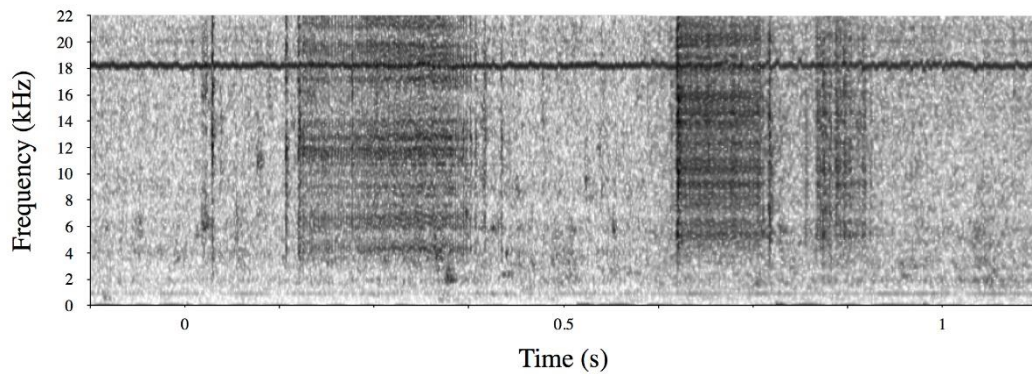


Figure 28 Spectrogram of pulsed sound “creak” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 18 kHz was an anomaly produced by the recording system.)

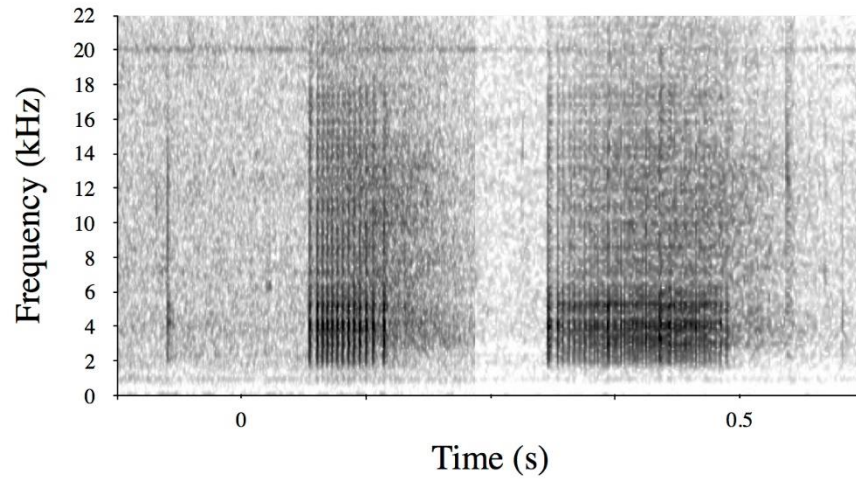


Figure 29 Spectrogram of pulsed sound “raspberry” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.)

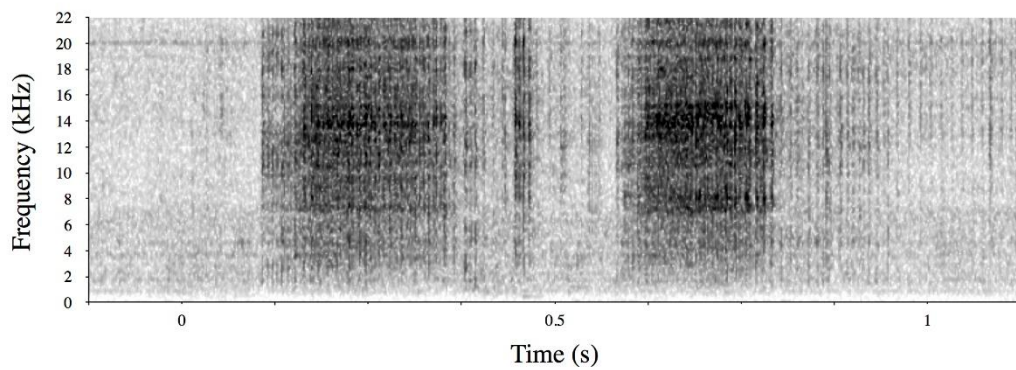


Figure 30 Spectrogram of pulsed sound “scrabble” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.)

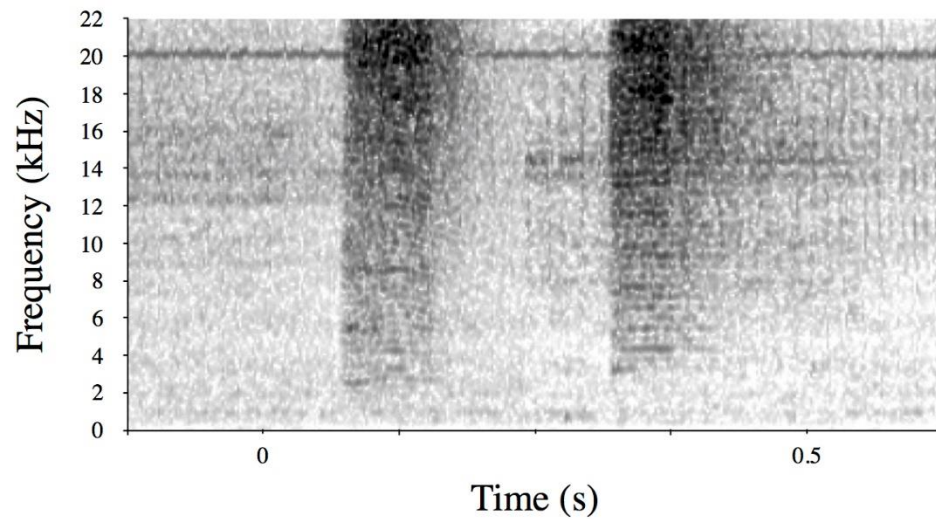


Figure 31 Spectrogram of pulsed sound “squeak” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.)

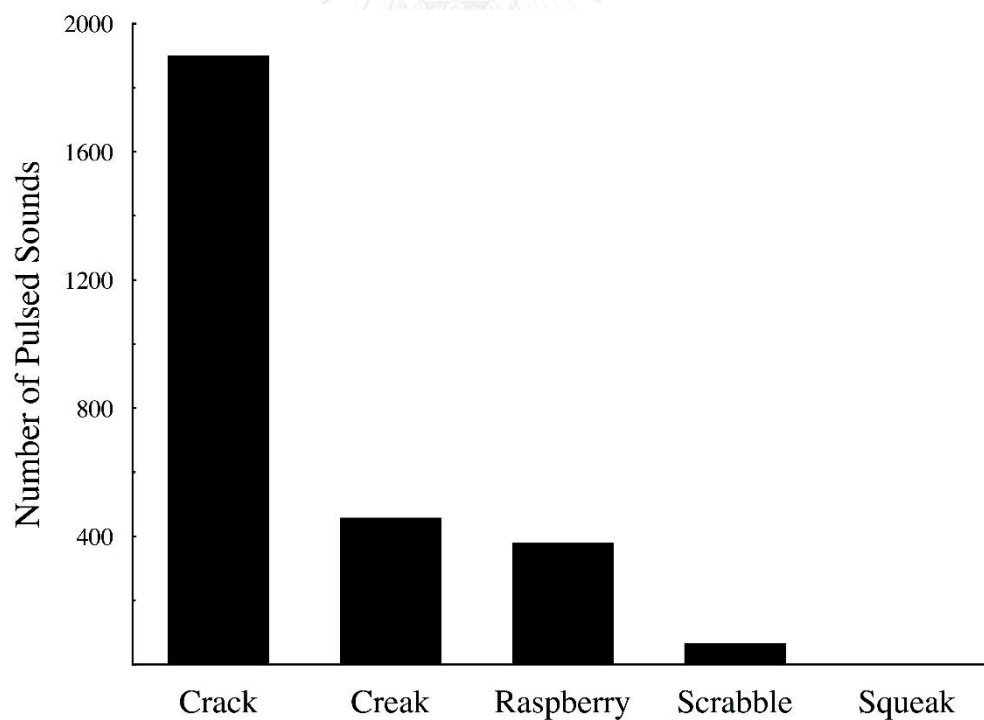


Figure 32 Number of five pulsed sounds types (crack, creak, raspberry, scrabble, and squeak) produced by three captive male Irrawaddy dolphins (*Orcaella brevirostris*) at Pattaya Dolphin World & Resort, Chonburi, Thailand in March and November 2014



Figure 33 Continuous shots (A-D) of aggression behaviours displayed by two captive male Irrawaddy dolphins (*Orcaella brevirostris*) — one dolphin swam quickly and charged another dolphin by leaping on it at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014.

3. Whistles

Whistles were the least frequent sound type recorded with a total of only 44 samples. All whistles were narrowband frequency-modulated sounds. Whistles were found to have diverse spectral contours that were categorized into nine types (Figures 34-43 & Table 2) — all were newly described and named based on their spectrogram contours.

Descriptions of all nine whistles types include: (1) Shriek: a single horizontally straight whistle moving slightly upward at the end of the contour with one harmonic (Figure 34); (2) Fall: a single whistle with slightly ascending contour at the first half and descending at the second half of the contour (Figure 35); (3) Flat: a single horizontally straight whistle with low frequency contour (1-4 kHz) (Figure 36); (4) Multi-Flat: multiple horizontally straight whistles with low frequency contours (1-7 kHz) (Figure 37); (5) Breaker: a single whistle with initially downward contour with two modulations (Figure 38); (6) Chirp: a very short single up-sweep whistle contour (Figure 39); (7) Harmonic: multiple of harmonic whistles all with initially rising contour and then constantly slightly upward or downward at the end of the contour (Figure 40); (8) Multi-Chirp: multiple of very short down-sweep harmonic contours (Figure 41); and (9) Multi-Loop: a single whistle starting with rising contour with multiple (2-7) modulations (Figure 42).

Generally, the frequency of whistles ranged from 1.1-20.6 kHz (6.7 ± 4.4) and could extend to above 22 kHz for the harmonic whistle type. The duration was 0.1-1.6 s (0.7 ± 0.4). The start, end, minimum, and maximum frequencies also varied depending

on the type of whistle, as shown in Table 2. Most of the whistles ($n = 33$) were heard during non-tourist sessions while the dolphins were swimming, whereas only a few were heard when dolphins regrouped following SWD and when they swam with the trainers.

4. Vocalization Rate

During tourist session, Irrawaddy dolphins produced 5,159 vocalizations (3.69 vocalization/min): 2,478 clicks (3.89 click/min), 2,665 pulsed sounds (4.23 pulse/min), and 16 whistles (0.15 whistle/min). On the other hand, during non-tourist session, Irrawaddy dolphins produced 1,590 vocalizations (2.61 vocalization/min): 1,420 clicks (3.49 click/min), 142 pulsed sounds (0.69 pulse/min), and 28 whistles (0.24 whistle/min) (Figures 44-45). Overall, Irrawaddy dolphins produced significantly higher ($p = 0.000009$) vocalization rate during tourist session. The numbers of clicks and pulsed sounds were significantly higher ($p < 0.05$) during tourist session; except whistles, which had no statistical difference between tourist and non-tourist sessions.

Table 2 Descriptive statistics for acoustic parameters of whistles (n = 44) with value given as mean \pm sd, including the associated behaviours, produced by three captive male Irrawaddy dolphins (*Orcaella brevirostris*) at Pattaya Dolphin World & Resort, Chonburi, Thailand in March and November 2014

Category	Number (T NT)	Duration (s)	Frequency Range (kHz)	Start Frequency (kHz)	End Frequency (kHz)	Minimum Frequency (kHz)	Maximum Frequency (kHz)	Behaviour
Breaker	1 (1 0)	0.9	9.6 - 12.1	12.1	10.3	9.6	12.1	I
Chirp	1 (1 0)	0.1	11.2 - 12	11.2	12	11.2	12	S
Fall	5 (0 5)	0.5 - 1.5 (1.1 \pm 0.4)	1.1 - 2.7	1.1 - 2.3 (2.0 \pm 0.5)	1.2 - 1.5 (1.4 \pm 0.2)	1.1 - 2.7 (1.6 \pm 0.7)	1.3 - 2.6 (2.3 \pm 0.6)	S
Flat	3 (0 3)	0.3 - 1.6 (0.9 \pm 0.7)	1.9 - 3.7	1.9 - 3.7 (2.9 \pm 0.9)	2.3 - 3.5 (3.0 \pm 0.6)	1.9 - 3.7 (2.9 \pm 0.9)	2.4 - 3.6 (3.2 \pm 0.7)	S
Harmonic	3 (1 2)	0.4 - 0.8 (0.6 \pm 0.2)	4.7 - 22	4.7 - 4.9 (4.8 \pm 0.1)	5.3 - 10.3 (7.2 \pm 2.7)	4.7 - 4.9 (4.8 \pm 0.1)	17.5 - 22 (20.5 \pm 2.6)	S
Multi-Chirp	2 (1 1)	0.1 - 0.2 (0.1 \pm 0.04)	3.8 - 20.6	3.8 - 14.8 (9.3 \pm 7.8)	6.3 - 11.5 (8.9 \pm 3.7)	3.4 - 5.7 (4.6 \pm 1.6)	17.6 - 20.6 (19.1 \pm 2.1)	I, S
Multi-Flat	12 (1 11)	0.2 - 0.7 (0.4 \pm 0.1)	1.8 - 6.1	1.8 - 4.8 (3.5 \pm 0.8)	2.2 - 5 (3.5 \pm 0.9)	1.8 - 3.7 (2.5 \pm 0.5)	4 - 6.1 (5.0 \pm 0.6)	S
Multi-Loop	16 (5 11)	0.7 - 1.3 (0.9 \pm 0.3)	2.3 - 12.3	2.3 - 10.9 (7.4 \pm 2.5)	8.9 - 11.7 (10.9 \pm 0.6)	2.3 - 11.7 (7.4 \pm 2.5)	11.2 - 12.3 (11.8 \pm 0.4)	I, Re, S
Shriek	1 (1 0)	0.7	7.5 - 16.7	7.5	8.6	7.5	16.7	R

Number: T = tourist session and NT = non-tourist session; Behaviours: A = aggression; F = feeding; I = interaction/physical contact; J = jumping; P = playing; S = swimming; SA = sexual arousal; So = socializing; TE = tourist-encounter; W = water spitting

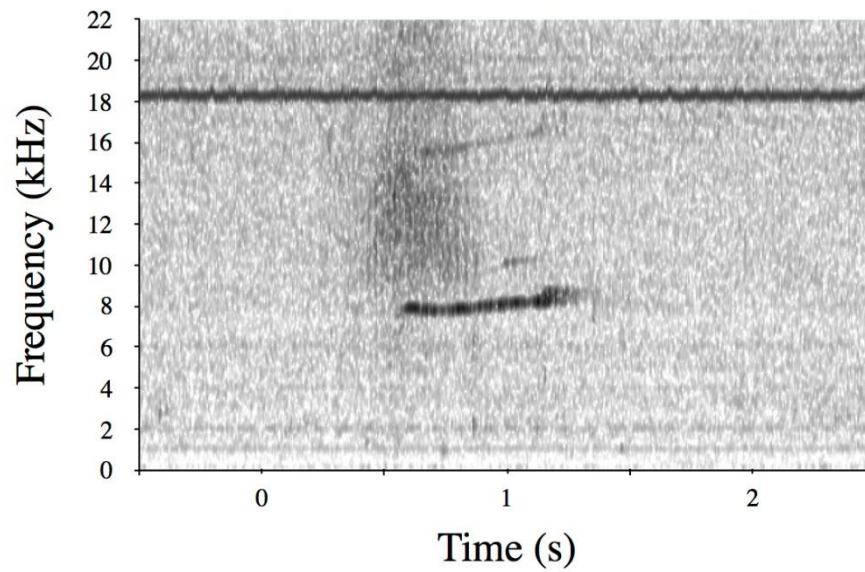


Figure 34 Spectrogram of whistle “shriek” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 18 kHz was an anomaly produced by the recording system.)

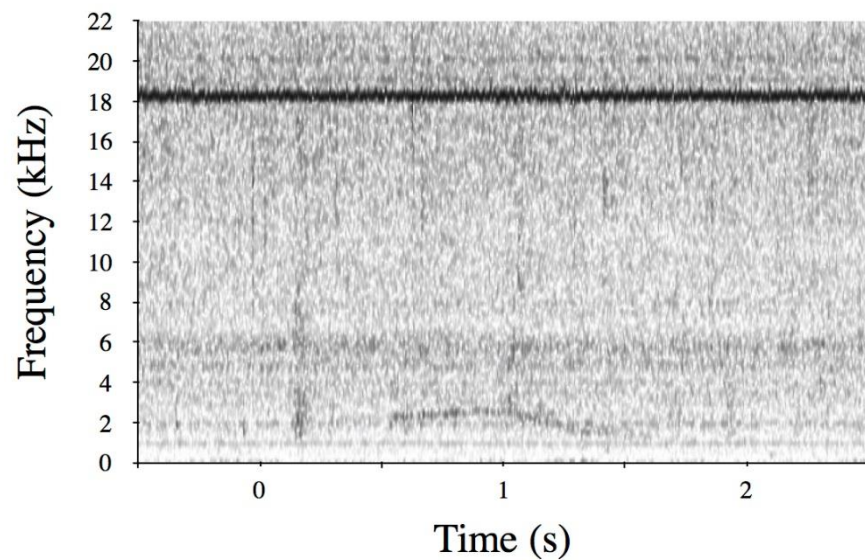


Figure 35 Spectrogram of whistle “fall” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 18 kHz was an anomaly produced by the recording system.)

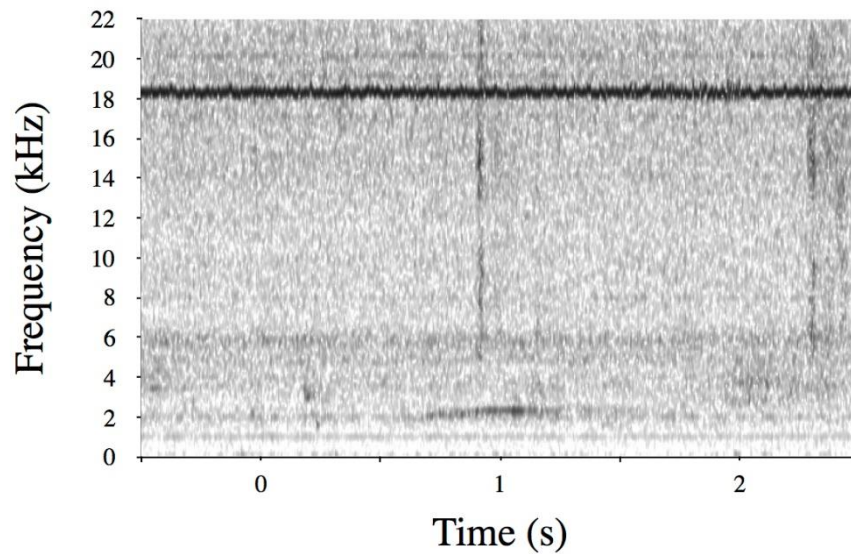


Figure 36 Spectrogram of whistle “flat” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014 (The intense narrowband frequency at 18 kHz was an anomaly produced by the recording system.)

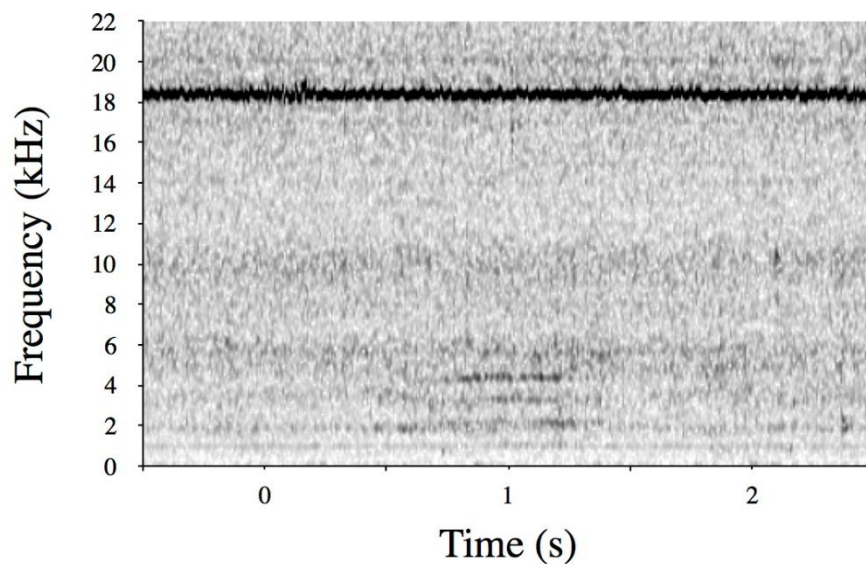


Figure 37 Spectrogram of whistle “multi-flat” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014 (The intense narrowband frequency at 18 kHz was an anomaly produced by the recording system.)

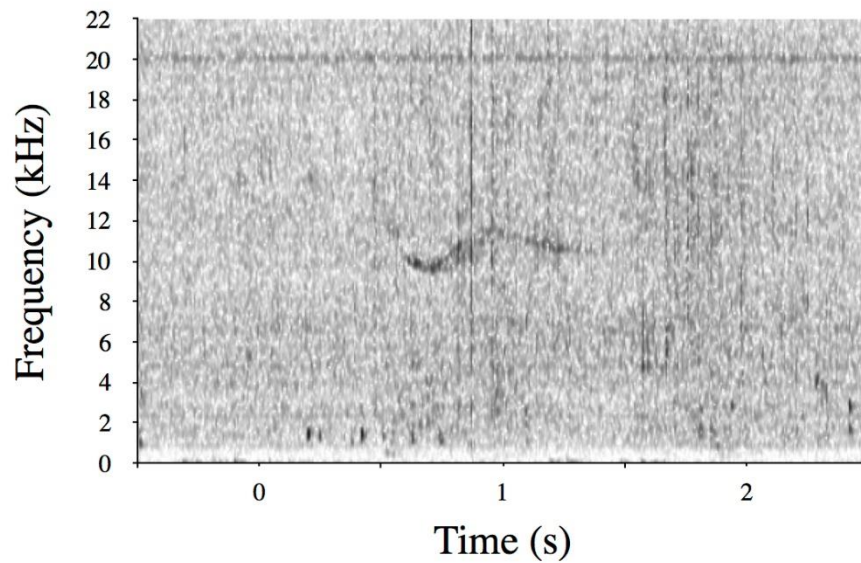


Figure 38 Spectrogram of whistle “breaker” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.)

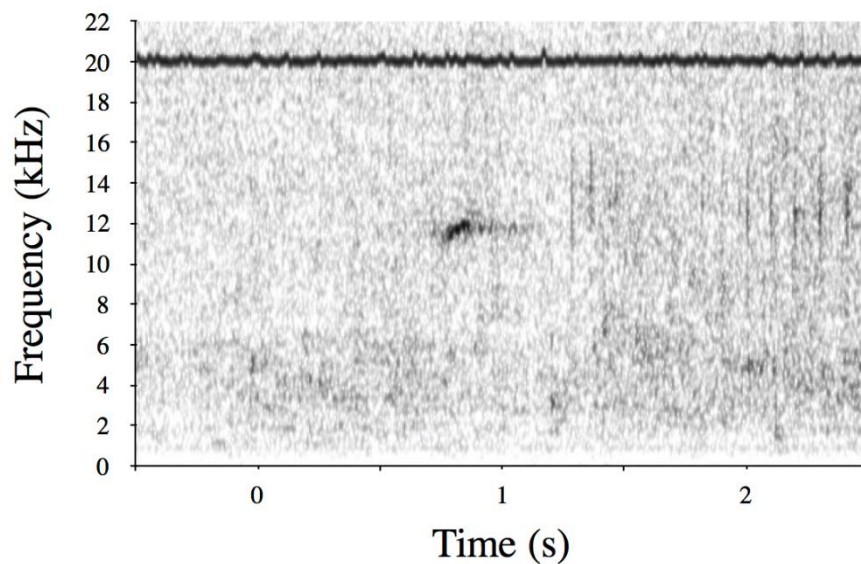


Figure 39 Spectrogram of whistle “chirp” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.)

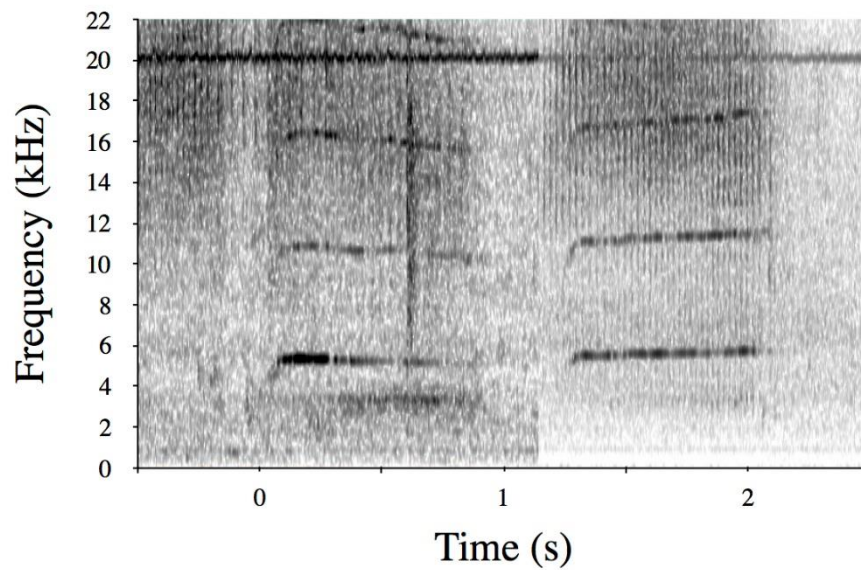


Figure 40 Spectrogram of whistle “harmonic” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.)

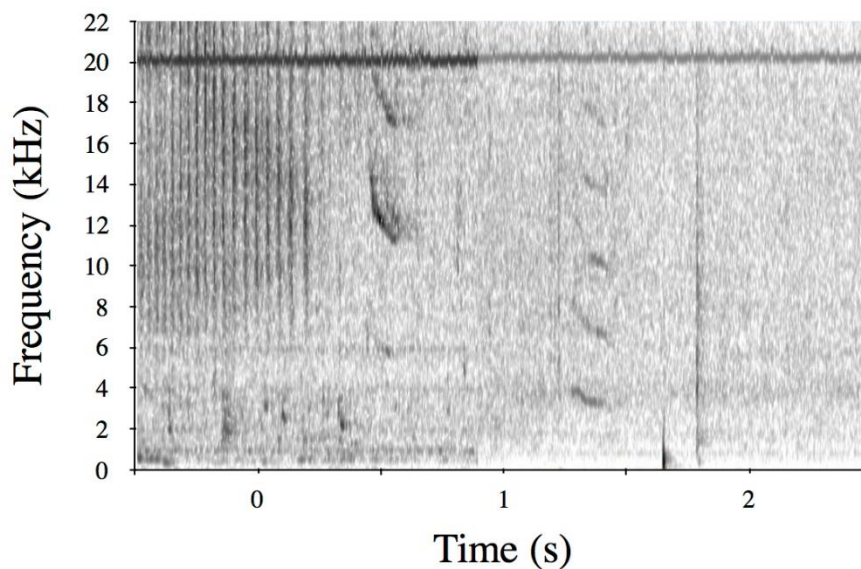


Figure 41 Spectrogram of whistle “multi-chirp” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in March 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.)

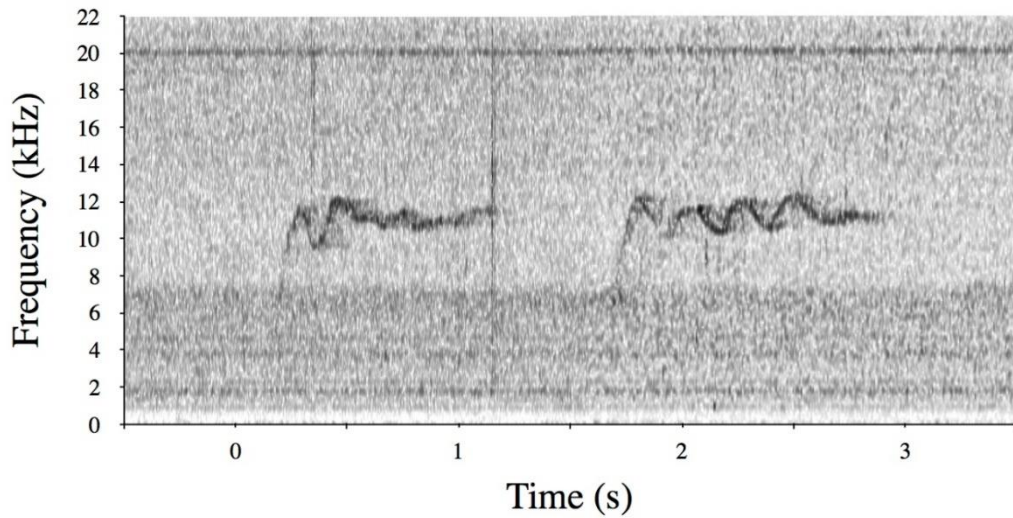


Figure 42 Spectrogram of whistle “multi-loop” produced by captive male Irrawaddy dolphin at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014 (The intense narrowband frequency at 20 kHz was an anomaly produced by the recording system.)

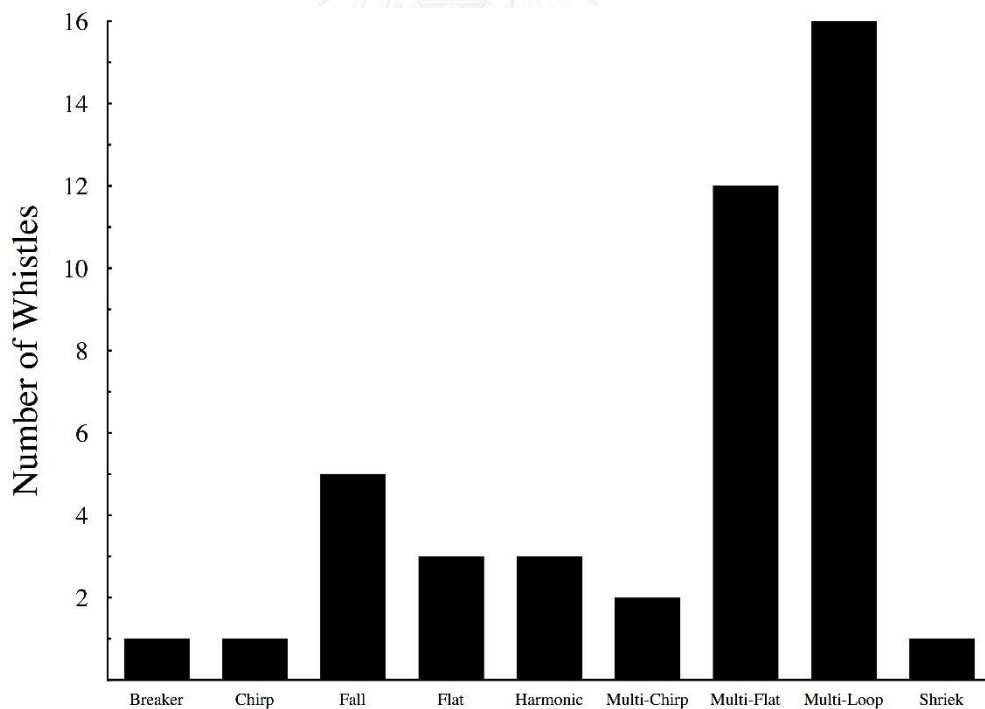


Figure 43 Number of nine whistles types (breaker, chirp, fall, flat, harmonic, multi-chirp, multi-flat, multi-loop, and shriek) produced by three captive male Irrawaddy dolphins (*Orcaella brevirostris*) at Pattaya Dolphin World & Resort, Chonburi, Thailand in March and November 2014

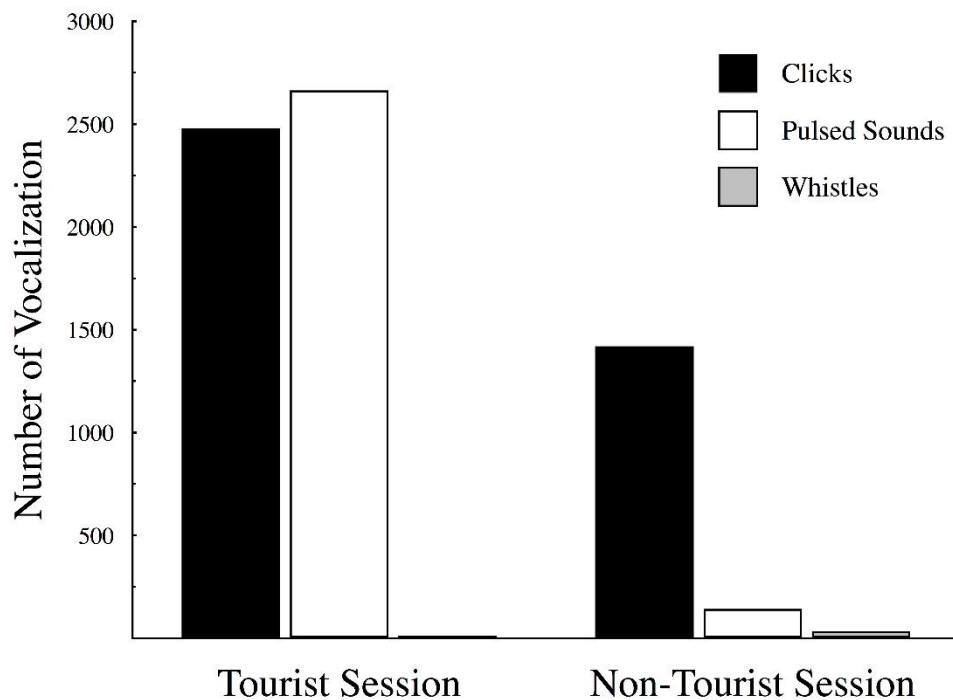


Figure 44 Number of vocalization (clicks, pulsed sounds, and whistles) produced by three captive male Irrawaddy dolphins (*Orcaella brevirostris*) during tourist and non-tourist sessions at Pattaya Dolphin World & Resort, Chonburi, Thailand in March and November 2014

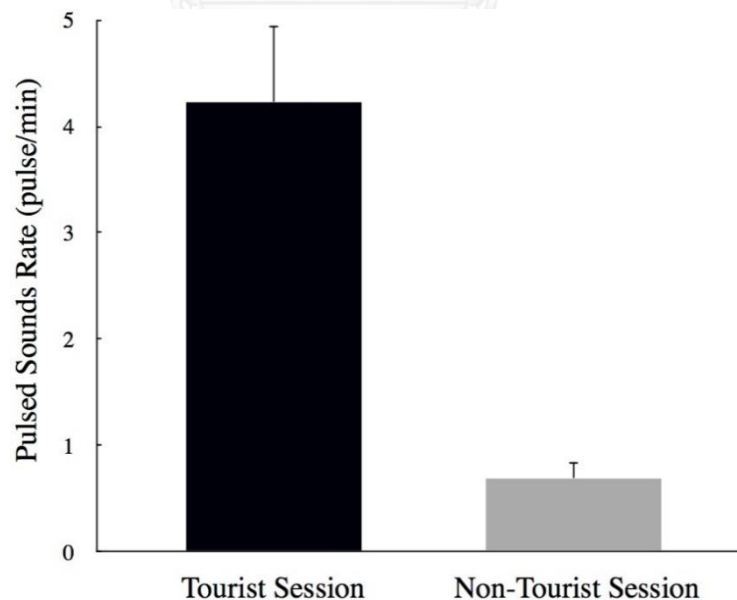


Figure 45 Pulsed sounds rate (pulse/min) produced by three captive male Irrawaddy dolphins (*Orcaella brevirostris*) during tourist and non-tourist sessions at Pattaya Dolphin World & Resort, Chonburi, Thailand in March and November 2014 (The lines on the top of the bar graph represent the standard error.)

CHAPTER 4

DISCUSSION

Captive Irrawaddy dolphins, like other delphinids, produced three types of sound: clicks, pulsed sounds, and whistles. This is the first study to capture all three sound categories (Frankel, 2009) within human audible range of captive Irrawaddy dolphins. The only previous captive study was able to record only pulse trains (Kamminga et al., 1983). Here, I discuss the similarities and differences of acoustic and physical behaviours of captive Irrawaddy dolphins compared to wild populations and other delphinid species.

1. Clicks

As with other delphinid species, captive Irrawaddy dolphins altered their clicks characteristics while echolocating at different distances from their targets. The repetition rate or ICI patterns could reflect how the dolphins used clicks to assess the distance between their positions and the positions of their targets, particularly clicks with fluctuating ICIs, which were regularly recorded while dolphins were approaching food items during feeding and objects (e.g., balls and flying discs) during playing behaviour.

In clicks with fluctuating ICIs (Figure 25), high repetition rate clicks at the beginning of train were normally recorded when objects were initially introduced to the pool; this initial phase of the train generally possess more energy, which would allow

the signals to travel further through water to locate unknown objects (Au & Würsig, 2004). In these cases, the intervals between clicks were simultaneously adjusted by emitting at rates that allowed the echo signals to return to the animals before the next click was emitted (Au & Benoit-Bird, 2003; Au & Würsig, 2004; Au, 2009). Therefore, this might explain why ICIs were decreasing while the dolphins were approaching the food items, which would be similar to the “Decreasing type” clicks reported in Commerson’s dolphins (*Cephalorhynchus commersonii*) (Yoshida et al., 2014).

Additionally, captive Irrawaddy dolphins did not use clicks as often as I expected despite the generally low visibility (2 m) within the pool. It is possible that the dolphins may have already memorized the entire small-and-non-complex geographic pool structure in which they have been living for four years, and therefore rely less on echolocation. Nonetheless, this assumption requires further studies.

2. Pulsed Sounds

Pulsed sounds produced by captive Irrawaddy dolphins were recorded mostly ($n = 2,665$) during tourist sessions. These pulsed sounds were associated with various behaviours, including aggression, sexual arousal, tourist-encounter, and resting behaviours.

2.1 Pulsed Sounds & Aggression

Squeaks (Figure 31) shared characteristic similarities to other burst-pulsed sounds produced by many dephinids, for instance, Hector’s dolphins (*Cephalorhynchus hectori*) (Dawson, 1991), Australian snubfin dolphins (Van Parijs et al., 2000),

bottlenose dolphins (Blomqvist & Amundin, 2004), spinner dolphins (*Stenella longirostris*) (Lammers et al., 2006), and dusky dolphins (*Lagenorhynchus obscurus*) (Au et al., 2010). Interestingly, it has been suggested that burst-pulsed sounds could be used by delphinids as a sonic weapon (Norris & Mohl, 1983; Marten et al., 1988). Furthermore, in consideration of the highly sensitive auditory system in delphinids (Au, 2009) combined with the fact that squeaks and burst-pulsed sounds were produced exclusively during aggression and socializing (Overstrom, 1983; Dawson, 1991; Blomqvist & Amundin, 2004; Lammers et al., 2006), it is possible that these pulsed sounds are intentionally used to cause auditory distress in the antagonists in addition to being used for expressing emotional states.

2.2 Pulsed Sounds & Sexual Arousal

Several delphinids have been reported to produce pulsed sound during sexual behaviours. For example, the pulsed sounds “pop” is used by bottlenose dolphins during courtship and/or dominant behaviours (Connor & Smolker, 1996), and “squawk” are used during sexual play (Herzing, 1996). Similarly, Atlantic spotted dolphins (*Stenella frontalis*) used high repetition-rate clicks called “buzz” and “squawk” during courtship and sexual play, respectively (Herzing, 1996). Excessive noises were also recorded in spinner dolphins during copulation (Silva Jr et al., 2005). Because captive Irrawaddy dolphins often produced pulsed sounds while they were performing their trained ejaculation behaviours with the veterinarians (Figure 22-23), it may be that pulsed sounds, especially cracks (Figure 27), were produced to express sexual emotions.

It is very interesting to understand the functionalities of these pulsed sounds such as the one concerned with sexual behaviours. By doing so, we may be able to develop an acoustic device for attracting wild Irrawaddy dolphins, or other endangered species, in order to increase mating success or to apply in population assessment, which all are regarding the conservative issues.

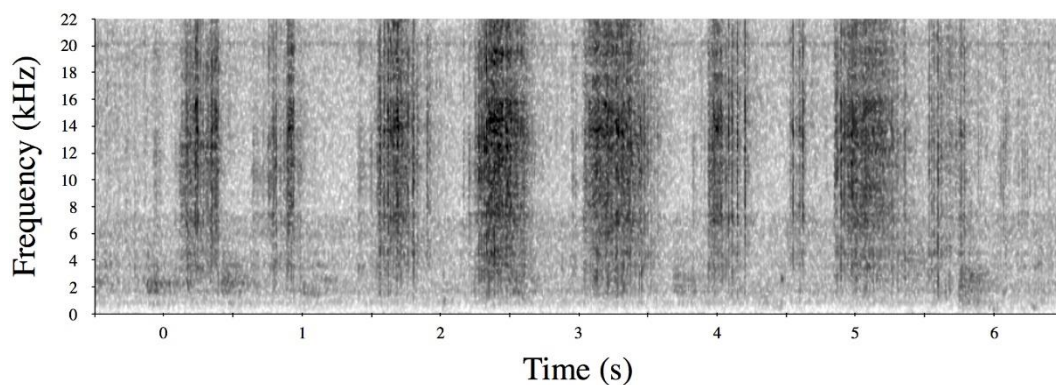


Figure 46 Spectrogram of an intense period of “pulsed sounds” rapidly produced by captive male Irrawaddy dolphin (*Orcaella brevirostris*) during tourist-encounter at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014

2.3 Pulsed Sounds & Tourist-Encounter

Tourist-encounter was the unique and the most interesting behaviour. All dolphins spontaneously swam toward the tourists, and emitted every kind of pulsed sounds when tourists were entering or leaving the pool and/or rotating their stations within the pool during the SWD (Figure 46). The pulsed sounds were rapidly produced. None of these intense periods of pulsed sounds were heard except during these particular circumstances. Moreover, the dolphins usually showed voluntary signs to interact with the tourists, and the animals continued to follow until all tourists left the pool area. These behaviours were similar to those reported in captive bottlenose

dolphins which showed frequent play behaviours and continued to voluntarily engage in activities with humans during “Dolphin Interaction Program” (Trone et al., 2005). Thus, these high activity periods during SWD potentially caused excitement for the dolphins, leading to excessive vocalizations, specifically the pulsed sounds which were directly related to emotional expression and social interaction.

2.4 Pulsed Sounds & Resting Behaviours

Resting behaviours (Figures 47-48) were often spotted during non-tourist session. Resting behaviours, such as sleeping (Figure 47) and slow swimming (or swim-rest) (Figure 48), are likely to vary on individual, and mostly exhibit during night time (Sekiguchi & Kohshima, 2003; Silva Jr et al., 2005; Trone et al., 2005). Although the observation was not allowed during night time, and there is scarce information provided in the wild, I suggest that frequent and long periods of resting behaviours (up to 1.5 minutes of sleeping) during day time could be caused by exhaustion and/or stress lasted from the showing activities, considering they had to participate in 40-minute-showtime for five rounds per day — and these low activity periods were the only time the animals could have rested or relaxed before the next show began. Consequently, these factors may as well explain why captive Irrawaddy dolphins showed extremely low pulsed sounds or any vocal production during non-tourist session.

Significantly low vocalization rate of pulsed sounds during non-tourist session; 2,665 samples (4.23 ± 0.7 pulse/min) during tourist session and only 142 samples (0.69 ± 0.2 pulse/min) during non-tourist session (Figure 45), could indicate low communication, social interaction, and emotional expression. Vocalization as well as

some vocal repertoires of delphinids can be lowered or altered by captivity where the following conditions are applied: space limitation, low diversification, low social interaction, and high stress (McCowan & Reiss, 1995; Sekiguchi & Kohshima, 2003). As reported by Sekiguchi & Kohshima (2003) in captive bottlenose dolphins, they also produced significantly less vocalization during low activity periods where the animals spent most of the time on sleeping or resting. Moreover, there were no tourists and excitement factors (feeding, interaction, jumping, and playing) to influence the vocalization. Yet, the presence of pulsed sounds and social interactions during non-tourist session exhibited that captive Irrawaddy dolphins still socialize with each other.

3. Whistles

Even though little is known about Irrawaddy dolphin's acoustic behaviours, they did produce whistles. Nevertheless, both wild populations of produced clicks, pulsed sounds, and whistles as often as clicks and pulsed sounds (Van Parijs et al., 2000; Krieb & Borsani, 2004). In contrast, in isolated (and small) areas, Irrawaddy dolphins produce lower numbers of whistles (Krieb & Borsani, 2004). This reduction in whistles in small areas is similar to what I observed in captive subjects, which produced only 44 whistles compared to higher numbers of clicks (3,898) and pulsed sounds (2,807) (Figure 44). Thus, it is possible that Irrawaddy dolphins genuinely produce low whistles in captivity, where space and social diversification are limited; this may explain why Kamminga et al. (1983) was unable to capture whistles by this captive species.

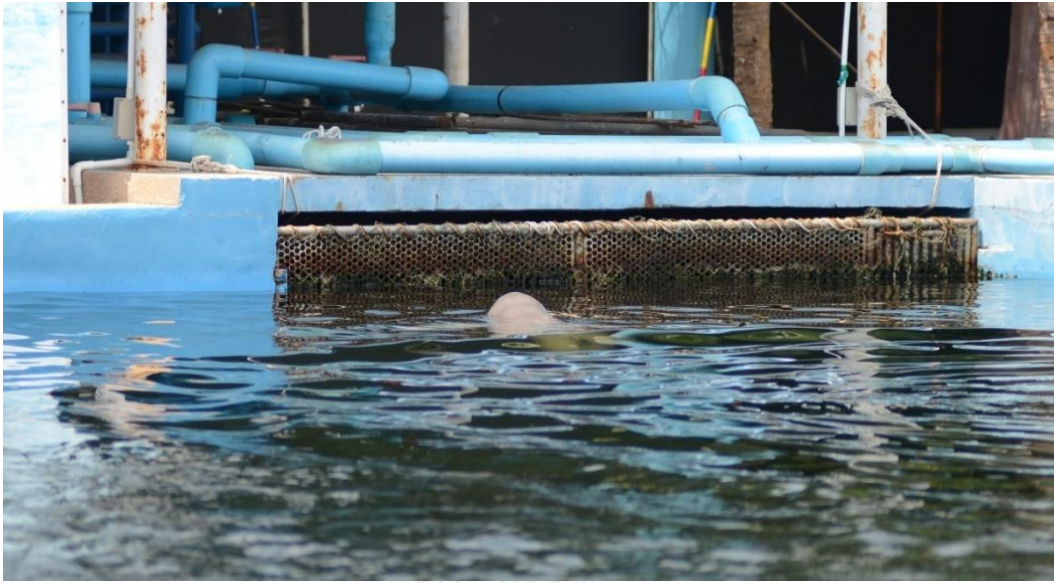


Figure 47 Resting behaviour/sleeping: the captive male Irrawaddy dolphins (*Orcaella brevirostris*) stopped swimming and stayed still while only the upper proportion of the head was displayed above the water surface during non-tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014.



Figure 48 Resting behaviour/slow swimming: the captive male Irrawaddy dolphin (*Orcaella brevirostris*) was swimming very slowly (almost staying still) while the upper proportion of the head and the body were displayed above the water surface during non-tourist session at Pattaya Dolphin World & Resort, Chonburi, Thailand in November 2014.

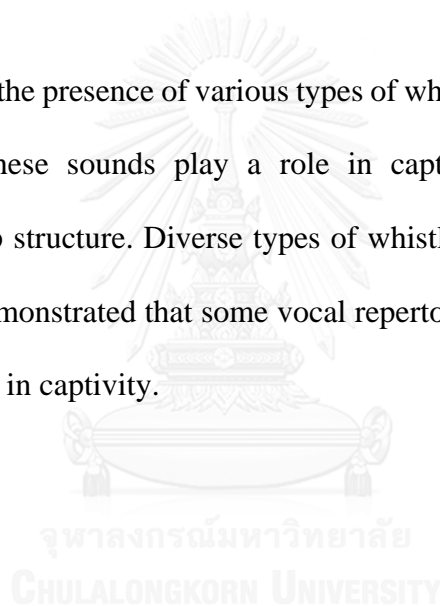
The extremely low number of whistles recorded in this study compared to the larger number of clicks and pulsed sounds could imply that the dolphins did not mainly rely upon whistles to establish contact or convey identities. Nonetheless, because limited social structure (only three individuals, all male) and enclosure area were available to our captive dolphins, I suggest that these animals, after years in captivity, no longer need to establish contact or identify themselves with whistles. Notwithstanding our hypothesis, comparative studies (e.g., with male-female compositions) would be necessary to ascertain its validity.

Furthermore, there were two contradictions in whistling behaviours between captive Irrawaddy dolphins and other wild delphinids. First, no whistles were recorded during feeding at all despite the fact that whistles were often observed during socializing and foraging in other delphinids (Van Parijs et al., 2000; Krieb & Borsani, 2004; Au et al., 2010; May-Collado & Wartzok, 2010; Henderson et al., 2012; Andrade et al., 2015). I suggest this disparity is because live prey was not available in captivity; food was given to the dolphins directly and there was an absence of group foraging/hunting behaviours which meant communication regarding feeding was likely to be unnecessary.

Second, numerous studies have shown that the whistling rate and the complexity of whistles are related to behavioural contexts and excitement level (Norris et al., 1994; Herzing, 1996; Frankel, 2009). Delphinids tend to produce less frequent and simple form whistles during low activity period: swimming, travelling, and resting — and vice versa during high activity period: foraging, socializing, fast movement, and aerial

behaviours (Herzing, 1996; Azevedo et al., 2010; Díaz López, 2011). Wild Irrawaddy dolphins were reported to produce whistles most frequently when (speed) boats were present, followed by foraging and socializing (Kreb & Borsani, 2004). Yet, most of the whistles produced by our subjects were heard during non-tourist sessions where the dolphins were typically swimming. Also, the complex multi-loop whistles with up to 4-7 modulations and harmonic whistles were mostly recorded during low activity periods. Hence, captivity may alter the properties of the whistles over time.

Nevertheless, the presence of various types of whistles, from simple to complex contours, suggests these sounds play a role in captivity in communication and maintenance of group structure. Diverse types of whistles with routine uses of clicks and pulsed sounds demonstrated that some vocal repertoires are still preserved despite long-term habituation in captivity.



CHAPTER 5

CONCLUSIONS

Captive Irrawaddy dolphins produced three sound categories, consisting of two types of clicks, five types of pulsed sounds, and nine types of whistles. Broadband clicks were directly related to feeding and swimming behaviours in navigational contexts. Pulsed sounds were produced in both narrowband and broadband signals with very short durations, high repetition rates, and high pulse rates. Pulsed sounds were associated with various behaviours relative to social and communicative contexts. Whistles, narrowband signals with frequency modulations, had the highest diversity, despite the fact that they were the least produced. Low whistling rates in captivity implied that captive Irrawaddy dolphins did not rely on whistles to communicate. Overall, vocalization rates were significantly higher during tourist sessions where many excitement factors were present, leading to excessive vocalizations, especially the pulsed sounds. Ultimately, captive Irrawaddy dolphins still have social interactions with each other and some vocal repertoires are still preserved even though the dolphins are habituated to, or even desensitized by, the dolphinarium where space and activity diversification are limited.

This study recorded clicks, pulsed sounds, and whistles within a frequency of 22 kHz, which does not include the complete bandwidth of this species. Further studies with broader bandwidth recording systems with a sample rate at least 300 kHz would complement and extend the current studies. Moreover, it is desirable to conduct more correlative studies of delphinid sounds and behaviours, both in captivity and in the wild.

It would be interesting to compare turbid and clean-sight captive environments and the differences between groups of only one sex and mixed sexes, as well as between small and large group sizes. Such studies would provide a foundation for evaluating the emotional state and vitality of delphinids that could enhance their welfare, which is especially important for endangered species such as the Irrawaddy dolphins.



REFERENCES

- Acevedo-Gutiérrez, A., & Stienessen, S. C. (2004). Bottlenose dolphins (*Tursiops truncatus*) increase number of whistles when feeding. *Aquatic Mammals*, 30(3), 357-362. doi:10.1578/AM.30.3.2004.357
- Amundin, M. (1991). *Sound production in odontocetes with emphasis on the harbour porpoise, Phocoena phocoena*.
- Andersen, S., & Pilleri, G. (1970). Audible sound production in captive *Platanista gangetica*. *Investigations on Cetacea*, 2, 83-86.
- Andrade, L. G., Lima, I. M. S., Bittencourt, L., Bisi, T. L., Júnior, J. L. B., & de Freitas Azevedo, A. (2015). High-frequency whistles of Guiana dolphins (*Sotalia guianensis*) in Guanabara Bay, southeastern Brazil. *The Journal of the Acoustical Society of America*, 137(1), 15-19. doi:10.1121/1.4902428
- Aroyan, J. L. (2001). Three-dimensional modeling of hearing in *Delphinus delphis*. *The Journal of the Acoustical Society of America*, 110(6), 3305-3318.
- Au, W. W. L. (1993). *The Sonar of Dolphins*: Springer-Verlag.
- Au, W. W. L., & Benoit-Bird, K. J. (2003). Automatic gain control in the echolocation system of dolphins. *Nature*, 423(6942), 861-863. doi:10.1038/nature01727
- Au, W. W. L., & Würsig, B. (2004). Echolocation signals of dusky dolphins (*Lagenorhynchus obscurus*) in Kaikoura, New Zealand. *The Journal of the Acoustical Society of America*, 115(5), 2307-2313. doi:10.1121/1.1690082
- Au, W. W. L. (2009). Echolocation. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of Marine Mammals* (2nd ed., pp. 348-357). London: Academic Press.
- Au, W. W. L., Lammers, M. O., & Yin, S. (2010). Acoustics of dusky dolphins (*Lagenorhynchus obscurus*). In B. Würsig, & M. Würsig (Eds.), *The Dusky Dolphin* (pp. 75-97). San Diego: Academic Press.
- Azevedo, A. F., & Simão, S. M. (2002). Whistles produced by marine tucuxi dolphins (*Sotalia fluviatilis*) in Guanabara Bay, southeastern Brazil. *Aquatic Mammals*, 28(3), 261-266. doi:10.1121/1.3308469
- Azevedo, A. F., Flach, L., Bisi, T. L., Andrade, L. G., Dorneles, P. R., & Lailson-Brito, J. (2010). Whistles emitted by Atlantic spotted dolphins (*Stenella frontalis*) in southeastern Brazil. *The Journal of the Acoustical Society of America*, 127(4), 2646-2651. doi:10.1121/1.3308469
- Beasley, I., Arnold, P., & Heinsohn, G. (2002). Geographical variation in skull morphology of the Irrawaddy dolphin, *Orcaella brevirostris* (Owen in Gray, 1866). *Raffles Bulletin of Zoology*, 15-34.
- Beasley, I., Robertson, K. M., & Arnold, P. (2005). Description of a new dolphin, the Australian snubfin dolphin *Orcaella heinsohni* sp. n. (Cetacea, Delphinidae). *Marine Mammal Science*, 21(3), 365-400. doi:10.1111/j.1748-7692.2005.tb01239.x
- Blomqvist, C., & Amundin, M. (2004). High-frequency burst-pulse sounds in agonistic/aggressive interactions in bottlenose dolphins, *Tursiops truncatus*. In C. Moss (Ed.), *Echolocation in Bats and Dolphins* (pp. 425-431). Chicago: The University of Chicago Press.
- Borsani, J. (1999). The Irrawaddy dolphins (*Orcaella brevirostris* Gray 1866) of Lao PDR: A visual-acoustic survey. *Environmental Protection and Community*

- Development in Siphandone Wetland Champassak Province, Lao PDR*
 Unpublished report of European Commission project Lao/B, 1-7.
- Caldwell, M. C., & Caldwell, D. K. (1965). Individualized whistle contours in bottlenosed dolphins (*Tursiops truncatus*). *Nature*, 207, 434-435.
- Caldwell, M. C., & Caldwell, D. K. (1967). Dolphin community life. *Los Ang. Cty. Mus. Nat. Hist. Contrib. Sci*, 5, 12-15.
- Caldwell, M. C., Hall, N. R., & Caldwell, D. K. (1972). *Ability of an Atlantic Bottlenosed Dolphin to Discriminate Between, and Respond Differentially to, Whistles of Eight Conspecifics*. Retrieved from
- Caldwell, M. C., Caldwell, D. K., & Tyack, P. L. (1990). Review of the signature whistle hypothesis for the Atlantic bottlenose dolphin, *Tursiops truncatus*. In S. Leatherwood, & R. Reeves (Eds.), *The Bottlenose Dolphin* (pp. 199-234). New York: Academic Press.
- Connor, R. C., & Smolker, R. A. (1996). 'Pop' goes the dolphin: A vocalization male bottlenose dolphins produce during consortships. *Behaviour*, 133(9), 643-662. doi:10.1163/156853996X00404
- Cranford, T. W. (1988). The Anatomy of Acoustic Structures in the Spinner Dolphin Forehead as Shown by X-Ray Computed Tomography and Computer Graphics. In P. E. Nachtigall, & P. W. B. Moore (Eds.), *Animal Sonar: Processes and Performance* (Vol. 156, pp. 67-77): Springer US.
- Cranford, T. W., Van Bonn, W. G., Chaplin, M. S., Carr, J. A., Kamolnick, T. A., Carder, D. A., & Ridgway, S. H. (1997). Visualizing dolphin sonar signal generation using high-speed video endoscopy. *The Journal of the Acoustical Society of America*, 102(5), 3123-3123. doi:10.1121/1.420593
- Cranford, T. W. (2000). In search of impulse sound sources in odontocetes *Hearing by whales and dolphins* (pp. 109-155). New York: Springer.
- Da Silva, V., & Best, R. (1994). Tucuxi *Sotalia fluviatilis* (Gervais, 1853). *Handbook of marine mammals*, 5, 43-69.
- Dawson, S. M. (1991). Clicks and communication: the behavioural and social contexts of Hector's dolphin vocalizations. *Ethology*, 88(4), 265-276. doi:10.1111/j.1439-0310.1991.tb00281.x
- Dawson, S. M., Barlow, J., & Ljungblad, D. (1998). Sounds recorded from Baird's beaked whale, *Berardius bairdii*. *Marine Mammal Science*, 14(2), 335-344.
- Deecke, V. B., & Janik, V. M. (2006). Automated categorization of bioacoustic signals: avoiding perceptual pitfalls. *The Journal of the Acoustical Society of America*, 119(1), 645-653.
- Díaz López, B., & Shirai, J. A. B. (2009). Mediterranean common bottlenose dolphin's repertoire and communication use. In A. G. Pearce, & L. M. Correa (Eds.), *Dolphins: Anatomy, Behavior, and Threats* (pp. 129-148). New York: Nova Science Publishers, Inc.
- Díaz López, B. (2011). Whistle characteristics in free-ranging bottlenose dolphins (*Tursiops truncatus*) in the Mediterranean Sea: Influence of behaviour. *Mammalian Biology - Zeitschrift für Säugetierkunde*, 76(2), 180-189. doi:10.1016/j.mambio.2010.06.006
- Dwass, M. (1960). Some k-sample rank-order tests. In I. Olkin (Ed.), *Contributions to probability and statistics* (pp. 198-202). Stanford, CA: Stanford University Press.

- Esch, H. C., Sayigh, L. S., Blum, J. E., & Wells, R. S. (2009). Whistles as potential indicators of stress in bottlenose dolphins (*Tursiops truncatus*). *Journal of Mammalogy*, 90(3), 638-650.
- Evans, W., & Awbrey, F. (1984). *High-Frequency Pulses of Commerson's Dolphins and Dall's Porpoise*. Paper presented at the American Zoologist.
- Evans, W., Awbrey, F., & Hackbarth, H. (1988). High frequency pulses produced by free-ranging Commerson's dolphin (*Cephalorhynchus commersonii*) compared to those of phocoenids. *Report of the International Whaling Commission Special(9)*, 173-181.
- Frankel, A. S. (2009). Sound production. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of Marine Mammals* (2nd ed., pp. 1056-1071). London: Academic Press.
- Henderson, E. E., Hildebrand, J. A., & Smith, M. H. (2011). Classification of behavior using vocalizations of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) a). *The Journal of the Acoustical Society of America*, 130(1), 557-567.
- Henderson, E. E., Hildebrand, J. A., Smith, M. H., & Falcone, E. A. (2012). The behavioral context of common dolphin (*Delphinus* sp.) vocalizations. *Marine Mammal Science*, 28(3), 439-460. doi:10.1111/j.1748-7692.2011.00498.x
- Herman, L. M., & Tavolga, W. N. (1980). The communication systems of cetaceans. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 149-209). New York: Wiley Interscience.
- Herzing, D. L. (1988). A quantitative description and behavioral associations of a burst-pulsed sound, the squawk, in captive bottlenose dolphins, *Tursiops truncatus*. *San Francisco State University*.
- Herzing, D. L. (1996). Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*. *Aquatic Mammals*, 22(2), 61-80.
- Herzing, D. L. (2000). Acoustics and social behavior of wild dolphins: implications for a sound society. In W. Au, A. N. Popper, & R. R. Fay (Eds.), *Hearing by whales and dolphins* (pp. 225-272). New York: Springer.
- Janik, V. M., & Slater, P. J. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal behaviour*, 56(4), 829-838. doi:10.1006/anbe.1998.0881
- Janik, V. M. (2000a). Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). *Science*, 289(5483), 1355-1357.
- Janik, V. M. (2000b). Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society of London B: Biological Sciences*, 267(1446), 923-927. doi:10.1098/rspb.2000.1091
- Janik, V. M., Sayigh, L. S., & Wells, R. (2006). Signature whistle shape conveys identity information to bottlenose dolphins. *Proceedings of the National Academy of Sciences*, 103(21), 8293-8297.
- Jensen, F. H., Rocco, A., Mansur, R. M., Smith, B. D., Janik, V. M., & Madsen, P. T. (2013). Clicking in shallow rivers: short-range echolocation of Irrawaddy and Ganges River dolphins in a shallow, acoustically complex habitat. *PloS one*, 8(4).

- Jing, X., Xiao, Y., & Jing, R. (1981). Acoustic signals and acoustic behaviour of Chinese river dolphin (*Lipotes vexillifer*). *Scientia Sinica*, 24(3), 407-415.
- Kamminga, C., Wiersma, H., & Dudok van Heel, W. H. (1983). Sonar sounds in *Orcaella brevirostris* of the Mahakam River, East Kalimantan, Indonesia; the first descriptions of the acoustic behaviour. *Aquatic Mammals*, 10, 83-95.
- King, S. L., Harley, H. E., & Janik, V. M. (2014). The role of signature whistle matching in bottlenose dolphins, *Tursiops truncatus*. *Animal Behaviour*, 96, 79-86. doi:10.1016/j.anbehav.2014.07.019
- Kreb, D., & Borsani, J. F. (2004). Impacts of habitat on the acoustic behaviour of coastal and freshwater Irrawaddy dolphins, *Orcaella brevirostris* in East Kalimantan, Indonesia. In D. Kreb (Ed.), *Facultative river dolphins: Conservation and social ecology of freshwater and coastal Irrawaddy dolphins in Indonesia* (pp. 161-184). Amsterdam: University of Amsterdam.
- Kruskal, W. H., & Wallis, W. A. (1952). Use of ranks in one-criterion variance analysis. *Journal of the American statistical Association*, 47(260), 583-621.
- Lammers, M. O., Schotten, M., & Au, W. W. (2006). The spatial context of free-ranging Hawaiian spinner dolphins (*Stenella longirostris*) producing acoustic signals. *The Journal of the Acoustical Society of America*, 119(2), 1244-1250. doi:10.1121/1.2151804
- Marten, K., Norris, K. S., Moore, P. W., & Englund, K. A. (1988). Loud impulse sounds in odontocete predation and social behavior. In P. E. Nachtigall, & P. W. B. Moore (Eds.), *Animal Sonar* (Vol. 156, pp. 567-579). New York: Plenum Press.
- May-Collado, L., & Wartzok, D. (2007). The freshwater dolphin *Inia geoffrensis geoffrensis* produces high frequency whistles. *The Journal of the Acoustical Society of America*, 121(2), 1203-1212.
- May-Collado, L., & Wartzok, D. (2010). Sounds produced by the tucuxi (*Sotalia fluviatilis*) from the Napo and Aguarico rivers of Ecuador. *Latin American Journal of Aquatic Mammals*, 8(1-2), 131-136. doi:10.5597/lajam00162
- McBride, A. F., & Hebb, D. O. (1948). Behavior of the captive bottle-nose dolphin, *Tursiops truncatus*. *Journal of comparative and physiological psychology*, 41(2), 111.
- McCowan, B., & Reiss, D. (1995). Whistle contour development in captive-born infant bottlenose dolphins (*Tursiops truncatus*): role of learning. *Journal of Comparative Psychology*, 109(3), 242.
- Morisaka, T., & Connor, R. (2007). Predation by killer whales (*Orcinus orca*) and the evolution of whistle loss and narrow-band high frequency clicks in odontocetes. *Journal of evolutionary biology*, 20(4), 1439-1458.
- Murray, S. O., Mercado, E., & Roitblat, H. L. (1998). Characterizing the graded structure of false killer whale (*Pseudorca crassidens*) vocalizations. *The Journal of the Acoustical Society of America*, 104(3), 1679-1688.
- Norris, K. S., & Mohl, B. (1983). Can odontocetes debilitate prey with sound? *American Naturalist*, 122(1), 85-104. doi:10.1086/284120
- Norris, K. S., Wursig, B., Wells, R. S., & Wursig, M. (1994). *The Hawaiian spinner dolphin*. Berkeley and Los Angeles, California: University of California Press.
- Oswald, J. N., Rankin, S., Barlow, J., & Lammers, M. O. (2007). A tool for real-time acoustic species identification of delphinid whistles. *The Journal of the Acoustical Society of America*, 122(1), 587-595.

- Overstrom, N. A. (1983). Association between burst-pulse sounds and aggressive behavior in captive Atlantic bottlenosed dolphins (*Tursiops truncatus*). *Zoo Biology*, 2(2), 93-103. doi:10.1002/zoo.1430020203
- Pilleri, G., Kraus, C., & Gahr, M. (1971). Physical analysis of the sounds emitted by *Platanista indi*. *Invest. Cetacea*, 3, 22-30.
- Podos, J., Da Silva, V. M., & Rossi-Santos, M. R. (2002). Vocalizations of Amazon river dolphins, *Inia geoffrensis*: insights into the Evolutionary origins of delphinid whistles. *Ethology*, 108(7), 601-612.
- Popper, A. N. (1980). Sound emission and detection by delphinids. *Cetacean behavior: Mechanisms and functions*, 1-52.
- Rankin, S., Oswald, J., Barlow, J., & Lammers, M. (2007). Patterned burst-pulse vocalizations of the northern right whale dolphin, *Lissodelphis borealis*. *The Journal of the Acoustical Society of America*, 121(2), 1213-1218. doi:10.1121/1.2404919
- Rasmussen, M. H., & Miller, L. A. (2002). Whistles and clicks from white-beaked dolphins, *Lagenorhynchus albirostris*, recorded in Faxaflói Bay, Iceland. *Aquatic Mammals*, 28(1), 78-89.
- Richardson, W., Greene, C., Malme, C., & Thomson, D. (1995). Marine mammals and noise Academic Press. *San Diego*.
- Rossi-Santos, M. R., Da Silva, J. M., Silva, F. L., & Monteiro-Filho, E. L. (2008). Descriptive parameters of pulsed calls for the spinner dolphin, *Stenella longirostris*, in the Fernando de Noronha Archipelago, Brazil. *Journal of the Marine Biological Association of the UK*, 88(06), 1093-1097.
- Sayigh, L., Tyack, P., Wells, R., & Scott, M. (1990). Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: Stability and mother-offspring comparisons. *Behavioral Ecology and Sociobiology*, 26(4), 247-260. doi:10.1007/BF00178318
- Sayigh, L., & Janik, V. M. (2009). Signature Whistles. In W. F. P. W. G. M. Thewissen (Ed.), *Encyclopedia of Marine Mammals (Second Edition)* (pp. 1014-1016). London: Academic Press.
- Sayigh, L., & Janik, V. (2010). Dolphin Signature Whistles. In M. D. B. Moore (Ed.), *Encyclopedia of Animal Behavior* (pp. 553-561). Oxford: Academic Press.
- Sekiguchi, Y., & Kohshima, S. (2003). Resting behaviors of captive bottlenose dolphins (*Tursiops truncatus*). *Physiology & Behavior*, 79(4-5), 643-653. doi:10.1016/S0031-9384(03)00119-7
- Silva Jr, J. M., Silva, F. J., & Sazima, I. (2005). Rest, nurture, sex, release, and play: Diurnal underwater behaviour of the spinner dolphin at Fernando de Noronha Archipelago, SW Atlantic. *Journal of Ichthyology and Aquatic Biology*, 9(4), 161-176.
- Simon, M., McGregor, P. K., & Ugarte, F. (2007). The relationship between the acoustic behaviour and surface activity of killer whales (*Orcinus orca*) that feed on herring (*Clupea harengus*). *Acta ethologica*, 10(2), 47-53.
- Smith, B. D., Thant, U. H., Lwin, J. M., & Shaw, C. D. (1997). Investigation of cetaceans in the Ayeyarwady River and northern coastal waters of Myanmar. *Asian Marine Biology*, 14, 173-194.

- Smith, B. D. (2009). Irrawaddy Dolphin: *Orcaella brevirostris*. In W. F. P. W. G. M. Thewissen (Ed.), *Encyclopedia of Marine Mammals (Second Edition)* (pp. 638-642). London: Academic Press.
- Smolker, R., Mann, J., & Smuts, B. (1993). Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behavioral Ecology and Sociobiology*, 33(6), 393-402. doi:10.1007/BF00170254
- Trone, M., Kuczaj, S., & Solangi, M. (2005). Does participation in Dolphin–Human Interaction Programs affect bottlenose dolphin behaviour? *Applied Animal Behaviour Science*, 93(3–4), 363-374. doi:10.1016/j.applanim.2005.01.003
- Tyack, P. L., Johnson, M. P., Zimmer, W. M., & Madsen, P. (2006). *Acoustic behavior of beaked whales, with implications for acoustic monitoring*. Paper presented at the OCEANS 2006.
- Van Parijs, S. M., Parra, G. J., & Corkeron, P. J. (2000). Sounds produced by Australian Irrawaddy dolphins, *Orcaella brevirostris*. *Journal of the Acoustical Society of America*, 108(4), 1938-1940. doi:10.1121/1.1289667
- Van Parijs, S. M., & Corkeron, P. J. (2001). Vocalizations and behaviour of Pacific humpback dolphins *Sousa chinensis*. *Ethology*, 107(8), 701-716. doi:10.1046/j.1439-0310.2001.00714.x
- Wang, D., Würsig, B., & Evans, W. (1995). Comparisons of whistles among seven odontocete species. *Sensory systems of aquatic mammals*, 299-323.
- Watwood, S. L., Tyack, P. L., & Wells, R. S. (2004). Whistle sharing in paired male bottlenose dolphins, *Tursiops truncatus*. *Behavioral Ecology and Sociobiology*, 55(6), 531-543. doi:10.1007/s00265-003-0724-y
- Watwood, S. L., Owen, E. C., Tyack, P. L., & Wells, R. S. (2005). Signature whistle use by temporarily restrained and free-swimming bottlenose dolphins, *Tursiops truncatus*. *Animal Behaviour*, 69(6), 1373-1386.
- Weilgart, L. S., & Whitehead, H. (1990). Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioral contexts. *Behavioral Ecology and Sociobiology*, 26(6), 399-402.
- Weir, C. R., Frantzis, A., Alexiadou, P., & Goold, J. C. (2007). The burst-pulse nature of ‘squeal’ sounds emitted by sperm whales (*Physeter macrocephalus*). *Journal of the Marine Biological Association of the United Kingdom*, 87(01), 39-46.
- Xiao, Y., & Jing, R. (1989). Underwater acoustic signals of the baiji, *Lipotes vexillifer*. *Biology and conservation of the river dolphins. Occas. Pap. IUCN Species Surv. Comm*, 3, 129-136.
- Yoshida, Y. M., & Morisaka, T., & Sakai, M., & Iwasaki, M., & Wakabayashi, I., & Seko, A., . . . Kohshima, S. (2014). Sound variation and function in captive Commerson's dolphins (*Cephalorhynchus commersonii*). *Behavioural Processes*, 108, 11-19. doi:10.1016/j.beproc.2014.08.017

APPENDIX



จุฬาลงกรณ์มหาวิทยาลัย
CHULALONGKORN UNIVERSITY

VITA